National Research Council Canada

Conseil national de recherches Canada

NRC · CNRC

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

http://cjfas.nrc.ca

http://jcsha.cnrc.ca

ISSN 0706-652X / CJFSDX 62(12) 2675–2900 (2005)

The *Canadian Journal of Fisheries and Aquatic Sciences*, previously published as *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, and *Journal of the Fisheries Research Board of Canada* 1938–1979, is issued monthly to form annual volumes of 12 numbers plus supplements.

Editorial policy. The Journal publishes original research articles, perspectives (syntheses, critiques, re-evaluations), discussions (comment and reply), and rapid communications. Manuscripts may concern cells, organisms, populations, communities, ecosystems, or processes that affect aquatic systems. They may cover a range of disciplines including biology and ecology of marine and freshwater organisms, limnology, oceanography, physiology, toxicology, genetics, economics, disease, and management. Preference will be given to manuscripts that emphasize understanding of observed phenomena and interpretation of experimental results. The Journal encourages papers that lead from clearly stated purpose or rationale and from testable hypotheses, concepts, or questions to identifiable conclusions or syntheses. Such papers may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. The Journal discourages papers that are essentially descriptive, except in emerging disciplines; have only site-specific or local applications (a certain year, place, taxon, chemical compound, etc.); only confirm previously established principles; or apply standard techniques without breaking new methodological ground.

Manuscripts for publication should be submitted to the Editorial Office via NRC Research Press' online submission and peer review system (**OSPREY**) at http://pubs.nrc-cnrc.gc.ca/cjfas/osprey. Alternatively, manuscripts may be submitted to the Senior Editor, *Canadian Journal of Fisheries and Aquatic Sciences*, Department of Integrative Biology, Building #006, Room 118, University of Guelph, Guelph, ON N1G 2W1, Canada (519-824-4120 ext. 52646; fax: 519-767-9798; e-mail: cjfas@uoguelph.ca).

Submissions in either English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor.

Correspondence concerning accepted manuscripts and corrected proofs should be sent to NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada (fax: 613-952-7656; e-mail: pubs@nrc-cnrc.gc.ca).

Instructions to Authors are published once a year in the first issue of each volume. Copies are available from NRC Research Press or at http://cjfas.nrc.ca. The **Publication Policy** of NRC Research Press is available at http://pubs.nrc-cnrc.gc.ca.

Microfilm. Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, USA.

US periodical postage paid at Champlain, NY 12919, USA, and at additional mailing offices. Attention US POSTMASTER: Send address changes to **Canadian Journal of Fisheries and Aquatic Sciences**, c/o USACAN Media Distribution Center, P.O. Box 2888, Plattsburgh, NY 12901, USA.

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, et *Journal of the Fisheries Research Board of Canada* 1938–1979. Le Journal paraît tous les mois, formant ainsi un volume de 12 numéros, et offre en plus jusqu'à deux suppléments par année.

Politique éditoriale. On publie, dans le Journal, des articles rendant compte de recherche originale, des perspectives (synthèses, critiques et réévaluations), des discussions (commentaires et réponses) et des communications rapides. Les documents peuvent porter sur les cellules, organismes, populations, communautés, écosystèmes ou processus qui affectent les systèmes aquatiques. Ils peuvent relever de divers domaines y compris la biologie et l'écologie des organismes marins et d'eau douce, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, la pathologie et la gestion. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux. On invite les auteurs à soumettre des articles ayant des objectifs précis ou relevant d'hypothèses, de concepts ou de questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. On décourage toutefois la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicables à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; et d'articles rendant compte de l'application de normes sans gain de méthodologie.

Les auteurs sont invités à soumettre leur **manuscrit** au Bureau de la rédaction par le truchement du Système de soumission et d'examen en direct des articles (**OSPREY**) des Presses scientifique du CNRC à http://pubs.nrc-cnrc.gc.ca/jcsha/osprey. Sinon, ils peuvent transmettre leur manuscrit par la poste à la directrice scientifique principale, *Journal canadien des sciences halieutiques et aquatiques*, Département de biologie intégrative, édifice 006, bureau 118, University of Guelph, Guelph, ON N1G 2W1, Canada (519-824-4120 poste 52646; télécopieur : 519-767-9798; courriel : cjfas@uoguelph.ca).

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à.-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le CNRC ne se tient en aucune façon responsable des opinions exprimées par un collaborateur ou des déclarations qui pourrait faire ce dernier.

La correspondance ayant trait aux manuscrits acceptés et les **épreuves corrigés** doivent être envoyées aux Presses scientifiques du CNRC, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada (télécopieur : 613-952-7656; courriel : pubs@nrc-cnrc.gc.ca).

Les Recommandations aux auteurs sont publiées une fois par année dans le premier numéro de chaque volume. Des copies sont disponibles auprès du Bureau de la rédaction aux Presses scientifiques du CNRC ou au http://jcsha.cnrc.ca. **La Politique de publication** est disponible auprès des Presses scientifiques du CNRC ou au http://pubs.nrc-cnrc.gc.ca.

Microfilms. On peut acheter sur microfilms de 16 ou 35 mm tous les numéros depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, É.-U.

This Journal is indexed or abstracted in / Cette revue est signalée ou résumée dans
ABSEARCH, Applied Science and Technology Index and Abstracts, Aquatic Sciences and Fisheries Abstracts, Biological Abstracts, Biological and Agricultural Abstracts, CAB Abstracts, Chemical Abstracts, Current Contents, Elsevier BIOBASE, Environmental Abstracts, ETDE Energy Database, General Science Index and Abstracts, GEOBASE, GeoRef, Life Sciences Collection, Meteorological and Geoastrophysical Abstracts, Oceanic Abstracts, PASCAL Database, and Science Citation Index.

Volume 62, Number 12, December 2005

Canadian Journal of Fisheries and Aquatic Sciences

Published by the National Research Council of Canada

Volume 62, numéro 12, décembre 2005

Journal canadien des sciences halieutiques et aquatiques

Publié par le Conseil national de recherches du Canada

Senior Editor / Directrice scientifique principale **Moira M. Ferguson**

Editors / Directeurs

Jeffrey A. Hutchings, *Dalhousie University, Halifax*

Pierre Pepin, *Northwest Atlantic Fisheries Centre, DFO/MPO, St. John's, Newfoundland*

W. Gary Sprules, *University of Toronto at Mississauga*

Assistant to the Editors / Adjointe aux directeurs scientifiques **Holly Foster**

Associate Editors / Directeurs scientifiques associés

D. Boisclair, *Université de Montréal*
U. Borgmann, *Environment Canada, Burlington*
M.J. Bradford, *DFO/MPO and Simon Fraser University*
S.E. Campana, *DFO/MPO, Dartmouth*
R. Carignan, *Université de Montréal*
G.T. Evans, *DFO/MPO, St. John's, Newfoundland*
K.T. Frank, *DFO/MPO, Dartmouth*
J.W.A. Grant, *Concordia University*
M.M. Hansen, *Danish Institute for Fisheries Research, Silkeborg, Denmark*
R. Hilborn, *University of Washington*
D.F. Houlihan, *University of Aberdeen*
F.A. Huntingford, *University of Glasgow*
J.M. Jech, *NFSC/NOAA, Woods Hole, Mass.*
B. Jonsson, *Norwegian Institute for Nature Research, Oslo, Norway*
K.A. Kidd, *University of New Brunswick*
D.L. MacLatchy, *University of New Brunswick, Saint John*
P. Magnan, *Université du Québec à Trois Rivières*
C.T. Marshall, *University of Aberdeen*
R.B. Millar, *University of Auckland, New Zealand*
W.P. Patterson, *University of Saskatchewan*
Y.T. Prairie, *Université du Québec à Montréal*
T.J. Quinn II, *University of Alaska–Fairbanks, Juneau, Alaska*
T.P. Quinn, *University of Washington*
C.W. Ramcharan, *Laurentian University*
J.S. Richardson, *The University of British Columbia*
B. Sainte-Marie, *DFO/MPO, Mont-Joli*
R.E.H. Smith, *University of Waterloo*
S.J. Smith, *DFO/MPO, Dartmouth*
E.B. Taylor, *The University of British Columbia*
W.F. Vincent, *Université Laval*
R.D. Vinebrooke, *University of Alberta*
C.J. Walters, *The University of British Columbia*
B. de Young, *Memorial University of Newfoundland*

NRC Research Press / Presses scientifiques du CNRC

Editor-in-Chief / Directeur scientifique en chef **Bruce P. Dancik**

Assistant Editor-in-Chief / Adjoint au directeur scientifique en chef **Iain E.P. Taylor**

Journals Program / Programme des revues

Fax / Télécopieur : 613-952-7656; e-mail / courriel : pubs@nrc-cnrc.gc.ca; URL / URL : pubs.nrc-cnrc.gc.ca

Director / Directeur **Cameron D. Macdonald**

Business Manager / Gestionnaire des affaires **Jason Charron**

Manager, Journals Program / Gestionnaire, Programme des revues **Carolyn Brown**

Managing Editor / Rédactrice administrative **Cecily M. Pearson** (613-993-9099)

Publication Officers / Agents de publication **Jennifer McColl, Thad Costigan**

Advertising and reprints / Annonces publicitaires et tirés à part **Roxanne Landriault** (613-990-2254)

Subscriptions / Abonnements **Eileen Evans-Nantais** (613-990-7873)

The National Research Council of Canada accepts no responsibility for statements or opinions expressed by a contributor. Acceptance of an advertisement, announcement, or other material does not imply endorsement by either the Journal's Senior Editor or the National Research Council.

© National Research Council of Canada 2005. All rights reserved.

No part of this publication may be reproduced, stored, or transmitted in any form or by any means, without the written permission of the publisher, except as stated below.

The National Research Council of Canada grants **permission*** to individuals to make single copies of articles for personal use. Any person may reproduce short excerpts from articles in the journal for any purpose that respects the moral rights of authors, provided that the source is fully acknowledged. As a courtesy, the consent of authors of such material should be obtained directly from the author.

Authorization to reproduce items for other than personal use, as stated above, is granted by the National Research Council of Canada provided that the copyright fee of $7.00 per copy is paid directly to CANCOPY, One Yonge Street, Suite 1900, Toronto, ON M5E 1E5, Canada.

*The above permission does not extend to other kinds of copying, such as copying for general distribution, for advertising, or promotional purposes, for creating new collective works, or for resale. For such copying, arrangements must be made with the publisher, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

Subscription information

The *Canadian Journal of Fisheries and Aquatic Sciences* (ISSN 0706-652X) is published monthly by the National Research Council of Canada. The 2005 annual subscription rates (second class postage) for Canada are $954CAN institutional and $295CAN personal, for US & foreign $954US institutional and $295US personal. For air mail add $150US to foreign rate. Canadian customers please include 7% GST (business no. 12149 1807 RT 0275). Subscriptions are entered for the calendar year. Remittances should be made payable to the Receiver General for Canada, credit NRC. Price for regular single issues: institutional, $110.00; personal, $35.00. Supplements will be priced separately. Special rates apply to members of Canadian scientific and engineering societies if they subscribe through their respective societies.

There are no refunds on cancelled subscriptions once delivery has begun. Claims for missing issues should be made within four months (N. America) or six months (outside N. America) following the date of publication. The publisher expects to supply missing issues only when losses have occurred in transit and when the reserve stock will permit. For change of address and subscription enquiries: Subscription Office, NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada; tel.: 613-993-9084; fax: 613-952-7656; e-mail: pubs@nrc-cnrc.gc.ca.

Microform backfiles are available from UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, USA, and Micromedia Ltd., 20 Victoria St., Toronto, ON M5C 2N8, Canada.

All issues of the *Canadian Journal of Fisheries and Aquatic Sciences* since 1996 are available on the Web. Pricing information can be found at http://pubs.nrc-cnrc.gc.ca.

Le Conseil national de recherches du Canada ne se tient en aucune façon responsable des opinions exprimées par un collaborateur ou des déclarations que pourrait faire ce dernier. La publication d'annonces publicitaires, d'avis et autres n'implique pas l'endossement de leur contenu par la directrice principale de la Revue ou le CNRC.

© Conseil national de recherches du Canada 2005. Tous droits réservés.

Il est interdit de reproduire, de sauvegarder ou de transmettre quelque partie de la présente publication dans quelque format ou de quelque façon sans le consentement écrit de l'éditeur, à l'exception des conditions suivantes.

Le Conseil national de recherches du Canada accorde aux particuliers le droit de faire des copies individuelles pour leur usage personnel. Toute personne peut reproduire de courts extraits des articles de la Revue pour autant que les droits moraux de l'auteur soient respectés et que la mention de provenance soit clairement indiquée. Il est de convenance de demander le consentement de l'auteur avant de faire mention de son travail.

On obtiendra l'autorisation de reproduire des articles à d'autres fins que l'usage personnel (tel qu'on l'a décrit ci-dessus) auprès du Conseil national de recherches du Canada pour autant que des redevances de droits d'auteurs de 7,00 $/copie soient versées au CANCOPY, 1, rue Yonge, bureau 1900, Toronto, ON M5E 1E5, Canada.

*La permission ci-dessus ne s'applique pas à la reproduction à grande échelle, telle que la reproduction aux fins de distribution générale, publicitaire ou promotionnelle, de compilation de nouveaux ouvrages collectifs ou de revente. Dans de tels cas, il faudra ratifier une entente particulière avec l'éditeur, le Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada.

Renseignements sur l'abonnement

Journal canadien des sciences halieutiques et aquatiques (ISSN 0706-652X) est une publication mensuelle du Conseil national de recherches du Canada. Le prix de l'abonnement annuel en 2005 au Canada (courrier de deuxième classe) est de 954 $CAN pour les organismes et de 295 $CAN pour les particuliers. À l'étranger (y compris les É.-U.), le prix de l'abonnement est de 954 $US pour les organismes et de 295 $US pour les particuliers. L'expédition par avion exige des frais de 150 $US en sus du prix d'abonnement à l'étranger. Les clients du Canada doivent ajouter la TPS de 7 % (numéro d'entreprise 12149 1807 RT 0275). Les abonnements sont pour l'année civile. Tout paiement doit être adressé au Receveur général du Canada, crédit du CNRC. Le prix par numéro est de 110 $ pour les organismes et de 35 $ pour les particuliers. Le prix des hors-série varie. Les membres des sociétés canadiennes de sciences et de génie bénéficient de taux préférentiels en s'abonnant via leurs sociétés respectives.

Aucun remboursement ne sera accordé ni aucune annulation acceptée une fois que les livraisons auront commencé. Les réclamations de numéros manquants devront être soumises dans les quatre mois (Amérique du Nord) ou dans les six mois (à l'extérieur de l'Amérique du Nord) suivant la date de publication. L'éditeur ne fournira de numéros manquants que si le document a été perdu pendant l'expédition et que si le stock le permet. Adressez tout changement d'adresse ou toute question quant à l'abonnement au : Bureau des abonnements, Presses scientifiques du CNRC, Conseil national de recherches Canada, Ottawa, ON K1A 0R6, Canada; téléphone : 613-993-9084; télécopieur : 613-952-7656; courriel : pubs@nrc-cnrc.gc.ca.

On peut obtenir les fichiers rétrospectifs sur **microforme** auprès de UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, É.-U., et auprès de Micromedia Ltée, 20, rue Victoria, Toronto, ON M5C 2N8, Canada.

À partir de 1996, tous les numéros de *Journal canadien des sciences halieutiques et aquatiques* sont accessibles sur le Web. On trouvera des renseignements sur les tarifs à http://pubs.nrc-cnrc.gc.ca.

Light intensity, salinity, and host velocity influence presettlement intensity and distribution on hosts by copepodids of sea lice, *Lepeophtheirus salmonis*

R.L. Genna, W. Mordue, A.W. Pike, and A.J. Mordue (Luntz)

Abstract: Intensity and distribution of presettlement by the copepodid of the sea louse, *Lepeophtheirus salmonis*, on smolts of its host Atlantic salmon, *Salmo salar*, were quantified for 27 infection regimes under controlled flume conditions. Each infection regime represented a level of interaction between three levels (low, medium, high) of the physical factors of light (10, 300, 800 lx), salinity (20‰, 27‰, 35‰), and host velocity (0.2, 7.0, 15.0 cm·s^{-1}). Light, salinity, and host velocity independently and interactively determined the distribution and number of presettled copepodids on hosts. Host surface area also influenced the number of attached preestablished copepodids. The distribution of presettled copepodids on the host body surface closely corresponded to that of settled copepodids and chalimi reported from other studies, with the greatest levels observed on the fins, in particular the dorsal, caudal, and pectoral fins. Copepodid presettlement occurred on the gills under all conditions. Differential presettlement, not selective mortality, probably produces the distribution pattern of settled stages seen in other studies.

Résumé : Nous avons quantifié l'intensité et la répartition de la pré-fixation des copépodites du pou de mer, *Lepeophtheirus salmonis*, sur les saumoneaux de l'hôte, le saumon atlantique, *Salmo salar*, sous 27 régimes infectieux dans des conditions contrôlées de canalisation artificielle. Chaque régime infectieux représente un degré d'interaction entre trois niveaux (faible, moyen, élevé) de facteurs physiques, soit la lumière (10, 300 et 800 lux), la salinité (20, 27, 35 ‰) et la vitesse de déplacement de l'hôte (0,2, 7,0, 15,0 cm·s^{-1}). La lumière, la salinité et la vitesse de l'hôte déterminent de façon indépendante et de façon interactive la répartition et la densité du nombre de copépodites en pré-fixation sur les hôtes. La surface externe de l'hôte affecte aussi le nombre de copépodites attachés en pré-fixation. La répartition des copépodites en pré-fixation sur la surface corporelle de l'hôte correspond à celles des copépodites et des larves chalimus signalées dans d'autres études, avec les plus grands nombres sur les nageoires, en particulier la dorsale, la caudale et les pectorales. La pré-fixation des copépodites se fait sur les branchies dans toutes les conditions. C'est probablement la pré-fixation différentielle et non la mortalité sélective qui explique les patrons de répartition des stades fixés observés dans les autres études.

[Traduit par la Rédaction]

Introduction

The sea louse, *Lepeophtheirus salmonis*, is a specific ectoparasite of several species of salmonids in the Northern Hemisphere and is a significant pest of farmed salmon, with infections costing the Scottish salmon industry alone £20–£30 million each year in production losses (Pike and Wadsworth 2000). Control strategies should incorporate an understanding of the infection dynamics of the planktonic copepodid, which completes transmission by locating and infecting a new host. *Lepeophtheirus salmonis* copepodids are envisaged to occur in spatially and temporally discrete patches of varying densities in inshore waters in and around marine sea lochs and estuaries through which young hosts forage and swim during seaward migrations (Costelloe et al. 1998*b*; McKibben and Hay 2004; Penston et al. 2004). Such patches can be simulated in a flume with static hosts exposed to a bloom of moving copepodids.

Experimental infections with *L. salmonis* copepodids have been conducted independently at different temperatures and salinities under laboratory conditions in unlit (Bron et al. 1991; Grimnes and Jakobsen 1996) or lit static water (Dawson et al. 1997; Finstad et al. 2000; Tucker et al. 2000) or in unlit flowing water (Bowers et al. 2000). None of these studies has investigated the interactive effects of varying levels of these factors on host attachment and they have identified only the intensity and distribution of successfully settled *L. salmonis* copepodids on a host, ignoring the critical phase of attachment before permanent settlement. Furthermore, artificial infection is unlikely to produce realistic patterns of initial attachment, as lower infection intensities and different distribution patterns of attached copepodids are observed on wild hosts (Dawson 1998; MacKenzie et al. 1998; Finstad et al. 2000) or caged hosts (Boxaspen 1997).

Received 11 July 2004. Accepted 11 April 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 24 October 2005.
J18217

R.L. Genna,[1] W. Mordue, A.W. Pike, and A.J. Mordue (Luntz). School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, AB24 2TZ, Scotland, UK.

[1]Corresponding author (e-mail: r.l.genna@btinternet.com).

 doi: 10.1139/F05-163 © 2005 NRC Canada

Lepeophtheirus salmonis copepodids are known to respond to light (Aarseth and Schram 1999; Novales Flamarique et al. 2000), salinity changes (Heuch 1995), water movements (Heuch and Karlsen 1997), pressure (Bron et al. 1993), and chemicals (R.L. Genna, W. Mordue, A.W. Pike, and A.J. Mordue (Luntz), unpublished data; R.J.E. Bailey, M.A. Birkett, A. Ingvarsdottir, A.J. Mordue (Luntz), W. Mordue, B. O'Shea, J.A. Pickett, and L.J. Wadhams, School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, Scotland AB24 2TZ, UK, unpublished data). Chemical cues dominate specificity during settlement of marine invertebrate larvae (see Pawlik 1992; Rodriguez et al. 1993). In *L. salmonis*, both adults and copepodids exhibit search patterns (R.L. Genna, W. Mordue, A.W. Pike, and A.J. Mordue (Luntz), unpublished; Devine et al. 2000) and directional responses (Ingvarsdottir et al. 2002; R.J.E. Bailey, M.A. Birkett, A. Ingvarsdottir, A.J. Mordue (Luntz), W. Mordue, B. O'Shea, J.A. Pickett, and L.J. Wadhams, unpublished data) to host odors of salmon. In the copepodid, such behavior may serve to bring individuals within the vicinity of potential hosts and switch on settlement behavior by which copepodids will initially attach to a host. Although previously not investigated, the initial phase of host attachment, henceforth termed presettlement, precedes the three phases of attachment described as occurring during host settlement (Bron et al. 1991).

Once activated by chemical cues (R.L. Genna, W. Mordue, A.W. Pike, and A.J. Mordue (Luntz), unpublished data), copepodid host-searching behavior will improve the likelihood of encounter and presettlement on a host. The intensity and distribution of presettled copepodids on a host are hypothesized to be influenced predominantly by interactive physical factors, as identified in flume studies for the settlement of marine larvae of annelids (Butman et al. 1988; Cha et al. 1991; Snelgrove et al. 1999), bivalve mollusks (Gregoire et al. 1996; Tamburri et al. 1996; Snelgrove et al. 1999), decapod crustaceans (Boudreau et al. 1990; Blackmon and Eggleston 2001), and copepod crustaceans (Fleeger et al. 1995) under realistic environmental conditions.

Hence, the aim of this study was to investigate the interactive effects of varying light intensity, salinity, and host swimming velocity on the intensity and distribution of presettlement of *L. salmonis* copepodids to host fish under moving water conditions.

Materials and methods

Copepodid culture

Copepodids were cultured from eggs removed from gravid female *L. salmonis* at a salmon farm at Loch Melfort (GB grid reference NM822116) on the west coast of Scotland after being transferred on ice to the Zoology Building, University of Aberdeen (Scotland). Copepodids were cultured under conditions of ambient light (16 h light – 8 h dark), temperature (10 °C), and salinity (35‰) in fresh, aerated seawater. All copepodids used in experiments originated from the same batch of egg strings collected on 28 April 2001. Copepodids were 24–48 h old when used and, to aid recognition, were stained with neutral red after the protocol of Anstensrud (1989) prior to use.

Flume setup and maintenance

An elliptical gray Perspex flume (inside diameter 200 mm, height 250 mm, length 4200 mm, volume 100 L) was used with a clear Perspex section in the raceway for observation of fish. For host infection within the flume, fish were confined within a clear Perspex infection tube (bore 100 mm, diameter 110 mm, length 300 mm) fitted between steel grids slotted into the raceway, which allowed smolts to swim. Laminar flow through the tube was achieved by use of a collimator placed upstream, while a filter (pore size 100 µm) was placed directly downstream of the infection tube to collect unattached copepodids.

Aerated, artificial seawater at constant temperature (10 ± 0.1 °C) was recirculated in the flume at variable flow rates by means of an attached recirculating system with pump (model PV71/6; Beresford Pumps, Coventry, UK) and by controlled opening of the connecting valves. Water velocity was monitored and maintained to within 0.1 cm·s^{-1} of the flow regime using a flow meter (model 801; Valeport Ltd., Dartmouth, Devon, UK). Lighting was artificial from overhead fluorescent lights, with the level of lighting controlled by setting the number of lamps illuminating the flume and monitored with a light meter (model Mastersix; Gossen, Nürnberg, Germany). Salinity was maintained to ±0.5‰ of the required level with Peacock's seamix salt using a refractometer (New S-100; Tanaka Sanjiro Co. Ltd., Japan).

Experimental design and infection regimes

Experiments were conducted over the period 30 April – 5 May 2001 in the Zoology aquarium, University of Aberdeen. A multifactorial randomized block design was used, with interaction between the three factors (salinity, light, host velocity), each at three levels (low, medium, high), resulting in 3^3 infection regimes. Ten smolts were infected for each of the 27 infection regimes, with fish selected at random from a stock of 300 smolts (weight, 187.1 ± 3.2 g; fork length, 25.9 ± 0.2 cm). Host swimming velocity was manipulated by maintaining a swimming host within the infection tube and altering current speeds in the flume (low, 0.2 cm·s^{-1}; medium, 7.0 cm·s^{-1}; high, 15.0 cm·s^{-1}) to reflect the range of recorded swimming speeds of Atlantic salmon, *Salmo salar*, smolts (Grottum and Sigholt 1998; Moore et al. 1998; Boucher and Petrell 1999). Salinity (low, 20‰; medium: 27‰; high, 35‰) and light (low, 10 lx; medium, 300 lx; high, 800 lx) were set at values known to affect *L. salmonis* copepodid behavior (Bron et al. 1993; Heuch 1995; Novales Flamarique et al. 2000). To ensure that copepodids were not functioning under conditions of physiological stress, they were exposed to experimental levels of light and salinity only during the infection protocol.

Infection protocol

Prior to each infection, a smolt was introduced into the infection tube by raising and lowering the steel grid and left to acclimate for 5 min. During infection, 1000 copepodids were introduced into the flume upstream of the collimator so that all copepodids were entrained in a laminar flow through the infection tube in a dispersed cloud. Each infection lasted 5 min, to flush unattached copepodids from the infection tube, after which the filter was removed and its contents dis-

© 2005 NRC Canada

carded. The infection tube was lifted from the water, the fish culled, and measurements of fork length (centimetres) and wet weight (grams) taken to allow calculation of surface area (surface area = $14.93 \times \text{weight}^{0.5869}$; B. O'Shea, A.J. Mordue (Luntz), R.J. Fryer, and I.R. Bricknell, School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, Scotland AB24 2TZ, UK, unpublished data). The number and location of copepodids presettled on the body surface (including gills) were recorded using a binocular microscope using the areas of the body specified by Bjørn and Finstad (1998): five fin areas (anal, caudal, dorsal (including the adipose), pectoral, pelvic), four body areas (anterior and posterior dorsal, anterior and posterior ventral), the head area, and the gills. Counts were summed for the four body regions (body, fins, gills, head) and per fish.

Statistical analyses

To allow comparison between regimes, we calculated total numbers of presettled copepodids as a proportion of the initial 1000 copepodids released, while the distribution of copepodids on each host body region was calculated as a proportion of the total number presettled per fish. The effects of the three physical factors and fish parameters (length, weight, surface area) on the overall level of presettlement (binomial family, logit link function) and on the distribution patterns of presettled copepodids between body areas (binomial family, logit link function) and body regions (Poisson family, log link function) were analyzed by generalized linear models using the software package RGui© (The Free Software Foundation, Inc., Boston, Massachusetts). Model fitting was conducted by sequential backward elimination of nonsignificant ($p > 0.05$) terms from a full model.

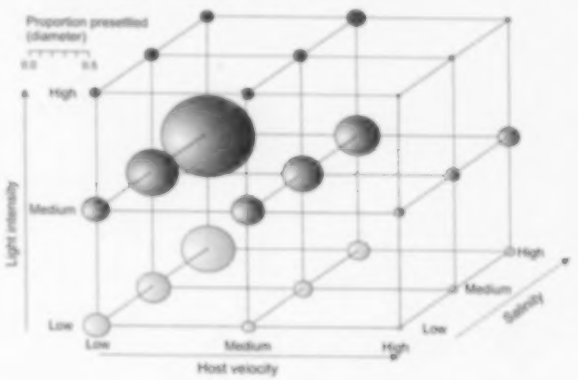
Results

Total presettlement

Light, salinity, and host velocity showed interactive effects in determining the proportion of presettled copepodids, with variability within and between infection regimes (Fig. 1). The generalized linear model showed good fit (null deviance, 37 665.50, 266 df; residual deviance, 1294.50, 239 df; Akaike's Information Criterion (AIC), 3060.90). In this model, the proportion of presettled copepodids was significantly determined by fish surface area (deviance, 1343.50, 1 df; AIC, 3107.90; $p < 0.001$) and the three factors with full interactions (deviance, 2001.90, 8 df; AIC, 3752.20; $p < 0.001$). Host surface area showed a negative relationship ($b = -7.756 \times 10^{-4} \pm 1.110 \times 10^{-4}$) with the total proportion of copepodids that presettled (P), such that $P = a\exp(b \times \text{surface area})$, where a is the number of copepodids that presettled under the interactive effects of light, salinity, and host velocity. For the small range in size of hosts used, variability in the proportion of presettled copepodids owing to host surface area was calculated as less than 0.005 (i.e., <0.5%); hence, the effects of surface area on presettlement were disregarded in this study.

Presettlement was maximal at medium light, low host velocity, and high salinity (0.708‰ ± 0.015‰) and minimal at high light, high host velocity, and low salinity (0.021‰ ± 0.001‰) (Fig. 1). Copepodid presettlement was influenced differently by each physical factor, greater at medium light intensity with sequentially fewer at low and high light intensity, greater at low to medium than high host velocity, and increasing with salinity for all regimes (Fig. 1).

Fig. 1. Mean proportion of *Lepeophtheirus salmonis* copepodids per infection that presettled on *Salmo salar* smolts exposed to one of 27 infection regimes ($n = 10$ per point). Each infection regime represents one combination of low, medium, and high levels of light (10, 300, 800 lx), salinity (20‰, 27‰, 35‰), and host velocity (0.2, 7.0, 15.0 cm·s^{-1}).



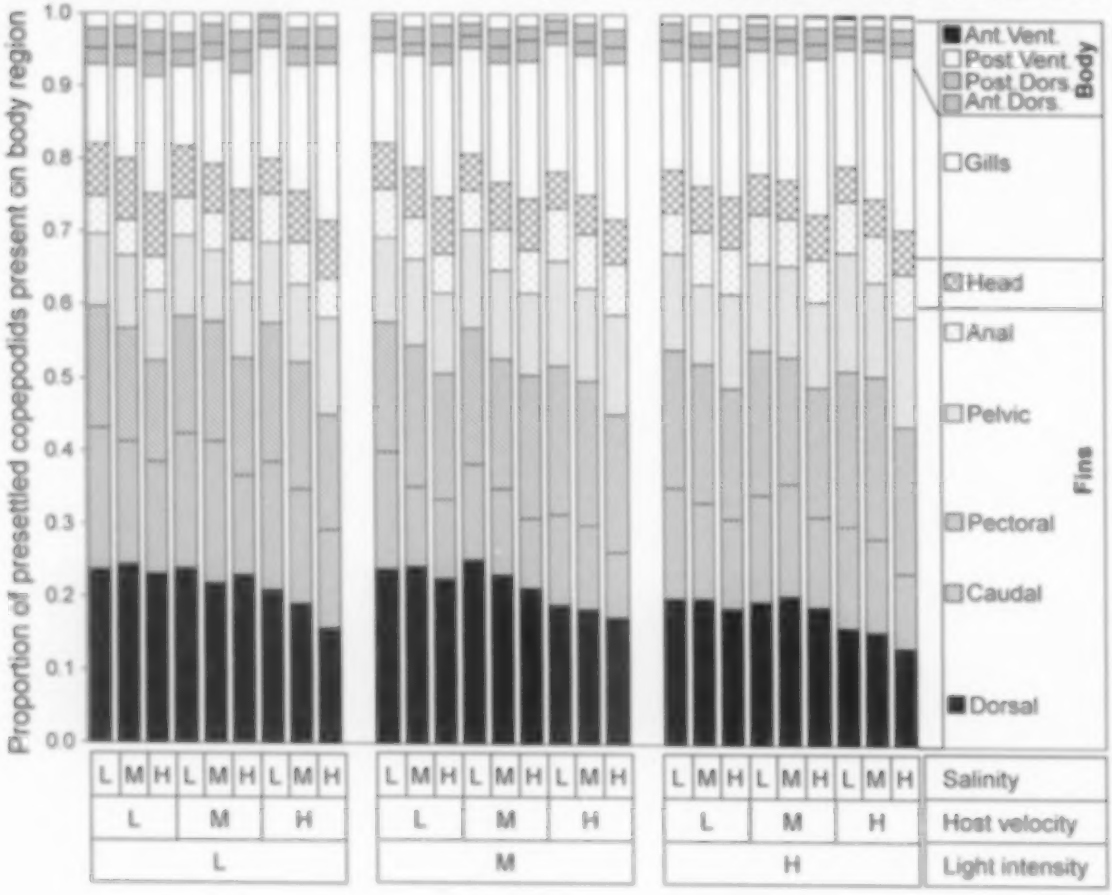
Presettled copepodid distribution

Presettled copepodids showed a differential distribution over the body surface of smolts under all regimes, both for individual areas (null deviance, 64 688.00, 2936 df; residual deviance, 11 160.10, 2902 df; AIC, 21817.10) and for grouped regions (null deviance, 71 245.80, 1067 df; residual deviance, 3539.80, 1035 df; AIC, 8608.90) of the host surface (Fig. 2). Differential presettlement occurred with greatest intensity on the fins and then the gills and head, with few on the body (Fig. 2). Specifically, the dorsal, caudal, and pectoral fins had greater intensities, with lower intensities on the pelvic and anal fins and the lowest intensity on the body (Fig. 2).

Physical factors determined the distribution of presettled copepodids on all body areas, but fish parameters did not ($p > 0.05$). Independent factors determined presettlement to all except two body areas (caudal and pectoral fins), where the interaction between factors was responsible. Light, host velocity, and salinity influenced presettlement on the gills ($p < 0.001$), the head ($p < 0.001$), and the body ($p < 0.001$), with only host velocity and salinity influencing presettlement on the fins ($p < 0.001$). Both light and host velocity determined presettlement on the anterior dorsal ($p < 0.05$) and posterior ventral ($p < 0.05$) body areas, with presettlement on the posterior dorsal body area determined by light ($p < 0.05$). Presettlement on the dorsal fin was independently influenced by all three factors ($p < 0.001$), while presettlement on the pelvic fins was independently influenced by salinity and light ($p < 0.001$). Presettlement on the pectoral and caudal fins was determined independently by light ($p < 0.001$) and interactively by host velocity and salinity ($p < 0.05$).

© 2005 NRC Canada

Fig. 2. Proportional distribution of presettled *Lepeophtheirus salmonis* copepodids between areas of the host (*Salmo salar* smolts) body surface for each of the 27 infection regimes. Each regime is the average of 10 fish ($n = 10$) infected at one combination of low (L), medium (M), and high (H) levels of light (10, 300, 800 lx), salinity (20‰, 27‰, 35‰), and host velocity (0.2, 7.0, 15.0 cm·s^{-1}).



The distribution of presettled copepodids changed between body regions with light (deviance, 3553.80, 2 df; AIC, 8619.00; $p < 0.001$) and host velocity (deviance, 3688.10, 2 df; AIC, 8753.20; $p < 0.001$) and between body areas with all three factors, with host velocity inducing the greatest effects (light: deviance, 11 169.00, 2 df, $p < 0.05$; salinity: deviance, 11 184.00, 2 df, $p < 0.001$; host velocity: deviance, 11 245.60, 2 df, $p < 0.001$).

Faster host velocity increased presettlement on the fins, particularly the dorsal and pectoral fins, but decreased presettlement on the gills, head, and body, reflecting the changes induced in individual body areas (Table 1). Greater salinity increased presettlement on the fins overall, with both increased (dorsal, caudal) and decreased (pelvic, pectoral) levels noted. Greater salinity also increased presettlement on the body and head but decreased presettlement on the gill tissues (Table 1). Increasing light intensity decreased gill presettlement but increased presettlement to the head and the body region, particularly on the anterior and posterior dorsal part of the body, and either increased (dorsal fin) or decreased (pectoral and pelvic fins) presettlement on individual fins but induced no overall effect on the fins as a group (Table 1).

Discussion

Light, salinity, and host swimming velocity interactively determined copepodid presettlement in this study, with almost all infection regimes showing different intensities. Presettlement showed a negative relationship with fish surface area, although this did not account for significant variability in the level of presettlement over the range of sizes of hosts used in this study. In a comparable study of *L. salmonis* settlement, no effect of surface area was found (B. O'Shea, A.J. Mordue (Luntz), R.J. Fryer, and I.R. Bricknell, School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, Scotland AB24 2TZ, UK, unpublished data). The decrease in presettlement with increasing host surface area in this study may reflect the greater increase in the body than the fins to the total host surface area, reinforced by the preference shown for presettlement on the fins.

© 2005 NRC Canada

Table 1. Outcomes of generalized linear models of physical factors affecting the distribution of *Lepeophtheirus salmonis* copepodid presettlement on *Salmo salar* smolts.

	Physical factor														
	Model fit, residuals			Light intensity				Host velocity				Salinity				
Region/area	AIC	Dev	df	AIC	Dev	*p*	Effect	AIC	Dev	*p*	Effect	AIC	Dev	*p*	Effect	Interactions
All fins	1440.0	86.0	262	—	—	ns	nc	1605.0	255.1	***	↑	1451.0	101.0	***	↑	NA
Dorsal fin	1413.4	121.4	260	1484.6	196.7	***	↑	1426.6	138.6	***	↑	1525.7	237.7	***	↑	NA
Caudal fin	1358.1	142.9	256	1474.0	262.8	***	Med ↓ High ↑	—	—	ns	↑	—	—	ns	↑	Yes[a]
Pectoral fins	1385.9	108.4	256	1413.6	140.2	***	↓	—	—	ns	nc	—	—	ns	↓	Yes[b]
Pelvic fins	1313.8	139.0	262	1333.6	162.8	***	↓	—	—	ns	nc	1334.3	163.5	***	↓	NA
Anal fin	—	—	—	—	—	ns	nc	—	—	ns	nc	—	—	ns	nc	NA
Gills	1351.9	100.5	260	1384.7	137.2	***	↓	1441.1	193.6	***	↓	1421.2	173.7	***	↓	NA
Head	1108.0	80.6	260	1120.8	97.4	***	↑	1123.0	99.6	***	↓	1123.4	99.9	***	↑	NA
Body	1111.2	103.1	260	1128.3	122.1	***	↑	1133.3	127.1	***	↓	1115.4	109.2	*	↑	NA
Anterior dorsal	837.6	91.8	262	841.4	99.5	*	↑	860.9	119.1	***	↓	—	—	ns	nc	NA
Posterior dorsal	858.2	109.4	264	863.2	118.4	*	↑	—	—	ns	nc	—	—	ns	nc	NA
Anterior ventral	—	—	—	—	—	ns	nc	—	—	ns	nc	—	—	ns	nc	NA
Posterior ventral	827.4	174.2	262	829.9	180.8	*	nc	834.1	184.9	**	↓	—	—	ns	nc	NA

Note: Independent factors showed 2 df with 4 df for interactions. Significance codes: not significant (ns), $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Changes in copepodid presettlement on each body region are shown in response to increasing levels of each significant factor (↑, increase; ↓, decrease; nc, no change). AIC, Akaike's Information Criterion; Dev, deviance; *p*, probability score of likelihood ratios; NA, not applicable.

[a]Host velocity and salinity (AIC = 1365.3, Dev = 158.3, $p < 0.05$), complex effects.

[b]Host velocity and salinity (AIC = 1387.5, Dev = 118.0, $p < 0.05$). Increase with salinity at low host velocity; increase with salinity at medium host veocity, mixed effects with host velocity at high salinity.

© 2005 NRC Canada

Although this study investigated copepodid presettlement, infection intensities compare well with the range of successful settlers recorded in artificial infections in low water flows with low (Bron et al. 1991; Grimnes and Jakobsen 1996) to high (Dawson et al. 1997; Finstad et al. 2000; Tucker et al. 2000) light conditions or low light and flowing water (Bowers et al. 2000) but are generally greater than those seen on wild hosts (Dawson 1998; MacKenzie et al. 1998; Finstad et al. 2000), which may reflect the high infection intensity used or indicate that more copepodids presettle than successfully settle on a host.

The environmental factors induced differential presettlement to areas of the host body, with the fins, particularly the dorsal, and the gills preferred. *Lepeophtheirus salmonis* settlement on wild hosts occurs predominantly on the fins, particularly the dorsal fin, with gill attachment seldom reported (Dawson 1998; MacKenzie et al. 1998; Finstad et al. 2000). Such infections occur at high salinity (>25‰) and under low light levels and during fast host swimming (Moore et al. 1998; Petersen and DeAngelis 2000). Comparable infection regimes in this study produced similar distribution but greater levels on the gills and pectoral fins and lower levels on the dorsal fin and body. These differences may be due to the swimming speeds being at the lower end of locomotory speeds for Atlantic salmon smolts in the wild (Grottum and Sigholt 1998; Moore et al. 1998; Boucher and Petrell 1999) or that the distribution of settled chalimi on wild hosts represents serial independent infections under different regimes. Hosts infected artificially in static water show chalimi predominantly settled on the gills and fins, particularly the dorsal fin, in lit tanks (Grimnes and Jakobsen 1996; Dawson et al. 1997; Bjørn and Finstad 1998) or the dorsal, ventral, and caudal fins and the gills in unlit tanks (Bron et al. 1991; Johnson and Albright 1991; Tucker et al. 2000). As in this study, low light intensity resulted in greater copepodid settlement on the ventral surfaces of paired fins and the entire caudal fin, the ventral flanks, opercula, and the gill filaments (Bron et al. 1991; Johnson and Albright 1991; Dawson et al. 1997).

The sites of copepodid presettlement will be determined by the copepodid's ability to attach to and remain on the host skin, with the suitability of a given area dependent on the nature of the epidermis and the degree of exposure to water currents (Bron et al. 1993). It may be a feature of the epidermis on the fins that allows more secure attachment than other areas, as differential settlement on the fins has been noted in other parasitic copepods, with local current speed, position maintenance in the host boundary layer, and movement towards areas of water movement proposed as factors during copepodid settlement in other parasitic copepods (Kabata and Cousens 1977; Boxshall 1976; Anstensrud and Schram 1988).

Detection of a swimming host by *L. salmonis* copepodids will predominantly involve the use of mechanical stimuli, namely the anterolateral flow field about a host, a low-frequency hydrodynamic dipole field derived from water being pushed ahead and along the sides of an advancing fish (Kalmijn 1989). Heuch and Karlsen (1997) showed that *L. salmonis* copepodids respond to uniform linear accelerations, similar to those found in front of a swimming fish, and suggested that copepodids react to such near-field accelerations produced within centimetres of a swimming fish with high-speed burst swimming and subsequent attachment to the host. The burst swimming response is likely to aid host attachment by increasing the chances of encountering a host or entering and remaining in the fish boundary layer, that region of reduced current flow and negligible current shear that exists around the host body. Copepodids may utilize the host boundary layer to facilitate presettlement on the host surface, and therefore, boundary layer dynamics will influence the distribution of presettled copepodids. This study supports this belief, with greater presettlement at slow swimming speeds when the boundary layer is thicker but declining at faster swimming speeds that thin the boundary layer. Faster host swimming may also change the flow field around a host, altering the distribution of copepodid presettlement. Increased, turbulent water flow would induce eddies behind fin regions and the fin rays, lying perpendicular to the current, and may provide shelter and hence make settlement in their lee easier (Bron et al. 1991). A thinner boundary layer would also reduce presettlement to areas without such eddies, namely the flanks and head, as in this study.

Conversely, increased water viscosity at higher salinity would thicken the boundary layer aiding copepodid attachment. This positive relationship between salinity and *L. salmonis* attachment has been reported previously (Tucker et al. 2000). Furthermore, as larval survival and development are affected by low salinity (<25‰), it will affect behavior and so presettlement (Johnson and Albright 1991). Low salinity may cause copepodids to sink or swim downwards and out of suspension, as observed in other meroplanktonic larvae during estuarine vertical migration, to locate deeper and more saline waters (reviewed by Forward 1987). This may explain the change in presettlement from the gills and ventral surfaces at low salinity to the head and dorsal surfaces at higher salinity as a function of increased copepodid activity and with less reliance on passive entrainment as described below.

Maximal copepodid presettlement occurred at low to medium light, with increasing light levels causing a shift in attachment from the ventral surfaces and fins to the head and dorsal and caudal areas and fins, indicative of a behavioral response to light. The structure of the visual system in *L. salmonis* copepodids allows location of a light or shadow source (Bron et al. 1993) and is sensitive to low light levels, such as those available during night time and crepuscular periods (Novales Flamarique et al. 2000), and may account for greater attachment at low to medium light intensity. Increased activity and the resultant higher position in the water column in response to rising light levels may account for a switch in distribution from ventral to dorsal surfaces. Poor presettlement at high light levels may reflect overstimulation of the visual system, with positive phototaxis known to occur in *L. salmonis* copepodids (Bron et al. 1993; Heuch 1995; Aarseth and Schram 1999).

The switch in presettled copepodids from ventral to dorsal surfaces and fins with increasing levels of salinity and light reflects their position in the water column from which they are able to attach to these areas. Changes in salinity and light induce the translocation of copepodids from ventral to dorsal areas of the body, mediated through increased copepodid activity and behavior.

© 2005 NRC Canada

To date, significant settlement on the gills has been observed only in laboratory infections, with the inference that settlement on the gills is a systematic artifact resulting from reduced host swimming speed and passive entrainment across the gills by the respiratory current (Bron et al. 1993; Tucker et al. 2000; Treasurer and Wadsworth 2004). This study partially supports this view, as the highest levels of presettlement on the gills occur under nonstimulatory conditions, namely static water and low light and salinity. However, although presettlement on the gills decreases at faster swimming speeds and higher salinities and light levels, it still persists under the most natural conditions. This suggests that presettlement on the gills is not an experimental artifact, despite infection levels greater than those observed in wild hosts infected at comparable swimming velocities. As such, initial gill attachment may be followed by selective removal–mortality mediated by water flow or host behavior. Other studies support this view, with reported changes in the intensity and distribution of attached copepodids over time after artificial infection (Bjørn and Finstad 1998) and total elimination from the gills 1–2 weeks postinfection (Dawson et al. 1997). Such a mechanism accounts for the respective greater and lesser copepodid presettlement on the gills and the rest of the body in this study in comparison with chalimi in other studies.

Given the influence of physical factors on successful copepodid presettlement, it is probable that copepodids exhibit behaviors to seek out areas with environmental conditions for optimal host attachment; namely medium to high salinity with low to medium light and slow host velocities. These conditions are found around estuarine haloclines at night when young hosts forage at slow speeds close to the water surface (Moore et al. 1998), with aggregations of *L. salmonis* copepodids previously reported in connection with such areas (Heuch 1995; Costelloe et al. 1998*a*, 1998*b*). These findings have implications for the siting of salmon farms in areas with physical conditions that minimize copepodid presettlement. Given that host swimming speed has the greatest influence on presettlement intensity, allowing greater host swimming speeds by siting salmon farms in areas of fast water currents or through lower stocking densities in individual pens may minimize the potential for farmed salmon to become infected. Siting of fish in pens at levels removed from the halocline or removed from the surface may also further reduce the overall intensity of sea lice presettlement on farmed salmonids.

In summary, light, salinity and host swimming velocity interactively affect the intensity and distribution of presettled *L. salmonis* copepodids on the body of a salmon by altering the boundary layer of fish hosts and the behavior of *L. salmonis* copepodids. Given the similarity between copepodid presettlement on all host body areas other than the gills in this study and the settlement of chalimi in other studies, it is proposed that the distribution on a host is predominantly produced by presettlement, with some differential mortality of copepodids presettled on the gills.

Acknowledgements

R.L.G was funded by the Natural Environment Research Council (GT04/1998/MS/007). We thank Lighthouse of Scotland for farm access for the collection of lice. Anna Ingvarsdóttir, Brid O'Shea, and Susan Robertson helped in the collection of egg strings and lice culture.

References

Aarseth, K.A., and Schram, T.A. 1999. Wavelength-specific behaviour in *Lepeophtheirus salmonis* and *Calanus finmarchicus* to ultraviolet and visible light in laboratory experiments (Crustacea: Copepoda). Mar. Ecol. Prog. Ser. **186**: 211–217.

Anstensrud, M. 1989. A vital stain for studies of behaviour and ecology of the parasitic copepod *Lernaeocera branchialis* (L.) (Penellidae). Mar. Ecol. Prog. Ser. **53**: 47–50.

Anstensrud, M., and Schram, T.A. 1988. Host and site selection by larval stages and adults of the parasitic copepod *Lernaeenicus sprattae* (Sowerby) (Copepoda, Penellidae) in the Oslofjord. Hydrobiologia, **167/168**: 587–595.

Bjørn, P.A., and Finstad, B. 1998. The development of salmon lice (*Lepeophtheirus salmonis*) on artificially infected post smolts of sea trout (*Salmo trutta*). Can. J. Zool. **76**: 970–977.

Blackmon, D.C., and Eggleston, D.B. 2001. Factors influencing planktonic, post-settlement dispersal of early juvenile blue crabs (*Callinectes sapidus* Rathbun). J. Exp. Mar. Biol. Ecol. **257**: 183–203.

Boucher, E., and Petrell, R.J. 1999. Swimming speed and morphological features of mixed populations of early maturing and nonmaturing fish. Aquacult. Eng. **20**: 21–35.

Boudreau, B., Bourget, E., and Simard, Y. 1990. Benthic invertebrate larval response to substrate characteristics at settlement — shelter preferences of the American lobster *Homarus americanus*. Mar. Biol. **106**: 191–198.

Bowers, J.M., Mustafa, A., Speare, D.J., Conboy, G.A., Brimacombe, M., Sims, D.E., and Burka, J.F. 2000. The physiological response of Atlantic salmon, *Salmo salar* L., to a single experimental challenge with sea lice, *Lepeophtheirus salmonis*. J. Fish Dis. **23**: 165–172.

Boxaspen, K. 1997. Geographical and temporal variation in abundance of salmon lice (*Lepeophtheirus salmonis*) on salmon (*Salmo salar* L.). ICES J. Mar. Sci. **54**: 1144–1147.

Boxshall, G.A. 1976. The host specificity of *Lepeophtheirus pectoralis* (Müller, 1776) (Copepoda: Caligidae). J. Fish Biol. **8**: 255–264.

Bron, J.E., Sommerville, C., Jones, M., and Rae, G.H. 1991. The settlement and attachment of early stages of the salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae), on the salmon host, *Salmo salar*. J. Zool. (Lond.), **224**: 201–212.

Bron, J.E., Sommerville, C., and Rae, G.H. 1993. Aspects of the behaviour of copepodid larvae of the salmon louse *Lepeophtheirus salmonis* (Krøyer, 1837). *In* Pathogens of wild and farmed fish: sea lice. *Edited by* G.A. Boxshall and D. Defaye. Ellis Horwood, London, UK. pp. 125–142.

Butman, C.A., Grassle, J.P., and Webb, C.M. 1988. Substrate choices made by marine larvae settling in still water and in a flume flow. Nature (Lond.), **333**: 771–773.

Cha, J.H., Bhaud, M., and Nattero, M.J. 1991. Experimental study of benthic recruitment in a hydrodynamic flume and in still water. C.R. Seances Acad. Sci. Ser. III Sci. Vie, **313**: 113–118.

Costelloe, M., Costelloe, J., Coghlan, N., O'Donohoe, G., and O'Connor, B. 1998*a*. Distribution of the larval stages of *Lepeophtheirus salmonis* in three bays on the west coast of Ireland. ICES J. Mar. Sci. **55**: 181–187.

Costelloe, M., Costelloe, J., Odonohoe, G., Coghlan, N.J., Oonk, M., and vanderHeijden, Y. 1998*b*. Planktonic distribution of sea lice larvae, *Lepeophtheirus salmonis*, in Killary Harbour, west coast of Ireland. J. Mar. Biol. Assoc. U.K. **78**: 853–874.

© 2005 NRC Canada

Dawson, L.H.J. 1998. The physiological effects of salmon lice (*Lepeophtheirus salmonis*) infections on returning post-smolt sea trout (*Salmo trutta* L.) in western Ireland, 1996. ICES J. Mar. Sci. **55**: 193–200.

Dawson, L.H.J., Pike, A.W., Houlihan, D.F., and McVicar, A.H. 1997. Comparison of the susceptibility of sea trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) to sea lice [*Lepeophtheirus salmonis* (Krøyer, 1837)] infections. ICES J. Mar. Sci. **54**: 1129–1139.

Devine, G.J., Ingvarsdottir, A., Mordue, W., Pike, A.W., Pickett, J., Duce, I., and Mordue (Luntz), A.J. 2000. Salmon lice, *Lepeophtheirus salmonis*, exhibit specific chemotactic responses to semiochemicals originating from the salmonid, *Salmo salar*. J. Chem. Ecol. **26**: 1833–1847.

Finstad, B., Bjorn, P.A., and Hvidsten, N.A. 2000. Laboratory and field investigations of salmon lice [*Lepeophtheirus salmonis* (Krøyer)] infestation on Atlantic salmon (*Salmo salar* L.) post-smolts. Aquacult. Res. **31**: 795–803.

Fleeger, J.W., Yund, P.O., and Sun, B. 1995. Active and passive processes associated with initial settlement and postsettlement dispersal of suspended meiobenthic copepods. J. Mar. Res. **53**: 609–645.

Forward, R.B., Jr. 1987. Crustacean larval migration: a perspective. *In* Signposts in the sea. Proceedings of a multidisciplinary workshop on marine animal orientation and migration. Department of Biological Science, Florida State University, Tallahasee, Fla.

Gregoire, Y., Bourget, E., and Verrette, J.L. 1996. Deposition of mimics of planktonic invertebrate larvae on simple and complex substrata in flume flows. Mar. Ecol. Prog. Ser. **135**: 89–100.

Grimnes, A., and Jakobsen, P.J. 1996. The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. J. Fish Biol. **48**: 1179–1194.

Grottum, J.A., and Sigholt, T. 1998. A model for oxygen consumption of Atlantic salmon (*Salmo salar*) based on measurements of individual fish in a tunnel respirometer. Aquacult. Eng. **17**: 241–251.

Heuch, P.A. 1995. Experimental evidence for aggregation of salmon louse copepodids (*Lepeophtheirus salmonis*) in step salinity gradients. J. Mar. Biol. U.K. **75**: 927–939.

Heuch, P.A., and Karlsen, H.E. 1997. Detection of infrasonic water oscillations by copepodids of *Lepeophtheirus salmonis* (Copepoda: Caligida). J. Plankton Res. **19**: 735–747.

Ingvarsdottir, A., Birkett, M.A., Duce, I., Genna, R.L., Mordue, W., Pickett, J.A., Wadhams, L.J., and Mordue (Luntz), A.J. 2002. Semiochemical strategies for sea louse control: host location cues. Pest Manag. Sci. **58**: 537–545.

Johnson, S.C., and Albright, L.J. 1991. Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda, Caligidae) under laboratory conditions. J. Mar. Biol. Assoc. U.K. **71**: 425–436.

Kabata, Z., and Cousens, B. 1977. Host–parasite relationship between sockeye salmon *Oncorhyncus nerka* and *Salmincola californiensis* (Dana, 1852) (Copepoda: Lernaeopodidae). J. Fish. Res. Board Can. **34**: 191–202.

Kalmijn, A.J. 1989. Hydrodynamic and acoustic field detection. *In* The mechanosensory lateral line. *Edited by* S. Coombs, P. Görner, and H. Münz. Springer-Verlag, New York. pp. 179–215.

MacKenzie, K., Longshaw, M., Begg, G.S., and McVicar, A.H. 1998. Sea lice (Copepoda: Caligidae) on wild sea trout (*Salmo trutta* L.) in Scotland. ICES J. Mar. Sci. **55**: 151–162.

McKibben, M.A., and Hay, D.W. 2004. Distributions of planktonic sea lice larvae *Lepeophtheirus salmonis* in the inter-tidal zone in Loch Torridon, western Scotland in relation to salmon farm production cycles. Aquacult. Res. **35**: 742–750.

Moore, A., Ives, S., Mead, T.A., and Talks, L. 1998. The migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts in the River Test and Southampton Water, southern England. Hydrobiologia, **371–372**: 295–304.

Novales Flamarique, I., Browman, H.I., Bélanger, M., and Boxaspen, K. 2000. Ontogenetic changes in visual sensitivity of the parasitic salmon louse *Lepeophtheirus salmonis*. J. Exp. Biol. **203**: 1649–1657.

Pawlik, J.R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr. Mar. Biol. Annu. Rev. **30**: 273–335.

Penston, M.J., McKibben, M.A., Hay, D.W., and Gillibrand, P.A. 2004. Observations on open-water densities of sea lice larvae in Loch Shieldaig, western Scotland. Aquacult. Res. **35**: 793–805.

Petersen, J.H., and DeAngelis, D.L. 2000. Dynamics of prey moving through a predator field: a model of migrating juvenile salmon. Math. Biosci. **165**: 97–114.

Pike, A.W., and Wadsworth, S. 2000. Sealice on salmonids: their biology and control. Adv. Parasitol. **44**: 233–337.

Rodriguez, S.R., Ojeda, F.P., and Inestrosa, N.C. 1993. Settlement of benthic marine invertebrates. Mar. Ecol. Prog. Ser. **97**: 193–207.

Snelgrove, P.V.R., Grassee, J.P., Grassle, J.F., Petrecca, R.F., and Hongguang, M. 1999. In situ habitat selection by settling larvae of marine soft-sediment invertebrates. Limnol. Oceanogr. **44**: 1341–1347.

Tamburri, M.N., Finelli, C.M., Wethey, D.S., and ZimmerFaust, R.K. 1996. Chemical induction of larval settlement behavior in flow. Biol. Bull. **191**: 367–373.

Treasurer, J.W., and Wadsworth, S.L. 2004. Interspecific comparison of experimental and natural routes of *Lepeophtheirus salmonis* and *Caligus elongatus* challenge and consequences for distribution of chalimus on salmonids and therapeutant screening. Aquacult. Res. **35**: 773–783.

Tucker, C.S., Sommerville, C., and Wootten, R. 2000. The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Krøyer, 1837) on Atlantic salmon, *Salmo salar* L. J. Fish Dis. **23**: 309–320.

© 2005 NRC Canada

Evidence across multiple scales for offshore transport of yellow perch (*Perca flavescens*) larvae in Lake Michigan

John M. Dettmers, John Janssen, Bernard Pientka, Richard S. Fulford, and David J. Jude

Abstract: Most freshwater fishes have short pelagic early life stages. Lake Michigan presents an interesting scenario for yellow perch (*Perca flavescens*), a species with a long pelagic larval stage that may not be well adapted to lakes with an expansive pelagic environment and extensive offshore transport. We investigated the possibility that early life stages of yellow perch were transported well offshore from their nearshore spawning grounds and explored whether food resources were more or less favorable offshore. To determine the extent to which pelagic age-0 yellow perch moved offshore, we sampled at multiple scales ranging from local (<2 km) to across the lake (>120 km). Evidence of offshore movement by fish larvae occurred at each scale. Yellow perch larvae were quickly transported offshore from nearshore spawning sites and remained in the offshore pelagia to sizes of at least 30 mm. Zooplankton density was greater offshore than nearshore, suggesting that pelagic age-0 yellow perch find improved food resources offshore compared with their nearshore spawning sites. Currents operating at oceanographic scales likely influenced the offshore movement of pelagic age-0 yellow perch in Lake Michigan. These currents, coupled with prey availability for pelagic age-0 individuals, may influence the recruitment success of this species.

Résumé : La plupart des poissons d'eau douce ont des premiers stades pélagiques de courte durée. Le lac Michigan présente un scénario intéressant pour la perchaude (*Perca flavescens*), une espèce avec un long stade larvaire pélagique, qui peut ne pas être bien adaptée à la vie dans des lacs qui ont un environnement pélagique étendu et un important transport vers le large. Nous avons vérifié la possibilité que les jeunes stades de la perchaude soient transportés bien au large depuis leurs lieux de ponte près du bord et nous avons examiné si les ressources alimentaires sont plus ou moins favorables au large. Afin de déterminer l'importance du déplacement des perchaudes pélagiques d'âge 0 vers le large, nous avons fait des échantillonnages à diverses échelles, allant de l'échelle locale (<2 km) à celle de la largeur du lac (>120 km). Il existe des indications de déplacement des larves de poissons vers le large à toutes les échelles. Les larves de perchaudes sont entraînées rapidement vers le large à partir des sites de ponte près des berges et ils demeurent dans les zones pélagiques au large jusqu'à la taille d'au moins 30 mm. La densité du zooplancton est plus grande au large que près du bord, ce qui laisse croire que les perchaudes pélagiques d'âge 0 trouvent au large des conditions de ressources alimentaires plus avantageuses que sur leurs sites de ponte près du bord. Les courants qui agissent à des échelles océaniques influencent vraisemblablement le déplacement des perchaudes pélagiques d'âge 0 vers le large dans le lac Michigan. Ces courants, combinés à la disponibilité des proies pour les individus pélagiques d'âge 0, peuvent influencer le succès du recrutement de cette espèce.

[Traduit par la Rédaction]

Received 29 September 2004. Accepted 27 May 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 28 October 2005.
J18329

J.M. Dettmers[1] **and B. Pientka.**[2] Lake Michigan Biological Station, Center for Aquatic Ecology, Illinois Natural History Survey, 400 17th Street, Zion, IL 60099, USA.
J. Janssen.[3] Department of Biology, Loyola University, 6526 N. Sheridan Road, Chicago, IL 60626, USA.
R.S. Fulford.[4] Department of Zoology, North Carolina State University, Campus Box 7617, Raleigh, NC 27595, USA.
D.J. Jude. School of Natural Resources and the Environment, 430 East University, University of Michigan, Ann Arbor, MI 48109, USA.

[1]Corresponding author (e-mail: dettmers@inhs.uiuc.edu).
[2]Present address: Vermont Department of Fish and Wildlife, 111 West Street, Essex Junction, VT 05452, USA.
[3]Present address: Great Lakes WATER Institute, 600 E. Greenfield Avenue, Milwaukee, WI 53204, USA.
[4]Present address: Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, MD 21037, USA.

 doi: 10.1139/F05-173 © 2005 NRC Canada

Table 1. Summary of the sampling scale, location of sampling, gear used, mesh sizes used, years and dates sampled, duration of each tow, and the crews that conducted each type of sampling for pelagic age-0 yellow perch (*Perca flavescens*) in southern Lake Michigan, 2000–2002.

Sample scale	Location	Gear	Mesh size (μm)	Year(s)	Dates	Duration (min)	Sample crew
Small scale	Evanston	N	500	1998–2000	May, June	5	Loyola
Small scale	Milwaukee	N	500	2001–2002	May, June	5	Loyola
Mesoscale	Waukegan	N	500, 1000, 1800	2000–2002	May–August	30	INHS
Mesoscale	Milwaukee	N, T	500, 1000	2001–2002	June–July	60, 30	NCSU (2001), Loyola (2002)
Cross-lake	Waukegan, Milwaukee, Muskegon	N	1000	2002	26–28 June	30	INHS, Loyola, UM

Note: N, 1 m × 2 m frame neuston net; T, 1 m × 0.5 m Tucker trawl; INHS, Illinois Natural History Survey; NCSU, North Carolina State University; UM, University of Michigan.

Introduction

Pelagic early life stages typically are very short in freshwater fishes (Houde 1994). Yellow perch (*Perca flavescens*) is an unusual freshwater fish in that, while its eggs are demersal and deposited in shallow water, it has a relatively long pelagic period spent offshore in ponds and medium to large lakes (Urho 1996). Typically, this period lasts 30–40 days before juveniles return to nearshore nursery areas (Whiteside et al. 1985). The practical effects of a long pelagic larval stage may have little impact on yellow perch when the nearshore–offshore distance is generally <1 km and depths are <20 m. For instance, larval yellow perch occurred well offshore in Oneida Lake (Houde 1969), a relatively large inland lake with a surface area of 207 km^2 (Clady and Hutchinson 1975). Houde (1969) suspected that these fish were transported offshore by currents, but year-class strength of yellow perch was driven primarily by walleye predation (Nielsen 1980). Similarly, most other studies concluded that biotic mechanisms, especially predation, limit recruitment of yellow perch (Johnson et al. 1992; Rudstam et al. 1996).

In the Great Lakes, predation remains the dominant mechanism cited in regulation of yellow perch year-class strength (Brandt et al. 1987; Hartman and Margraf 1993; Shroyer and McComish 2000), but these studies were in shallow portions of lakes or in embayments. Moreover, recruitment of yellow perch in Lakes Erie and St. Clair was influenced by water temperature (Henderson and Nepszy 1985). In the much larger Lake Michigan (surface area = 57 753 km^2), both biotic (e.g., maternal effects, Heyer et al. 2001; prey availability, Dettmers et al. 2003; predation, Shroyer and McComish 2000) and abiotic (e.g., water temperature and currents, Clapp and Dettmers 2004) mechanisms likely affect recruitment of yellow perch. Typically, yellow perch larvae have been sampled only very close to shore in Lake Michigan (Marsden and Robillard 2004). Thus, whether pelagic age-0 yellow perch consistently move well offshore in this very large lake system remains uncertain. However, age-0 yellow perch have been incidentally observed offshore, primarily in July and August (Nash and Geffen 1988). Similarly, we have observed age-0 yellow perch offshore as much as 56 km from the Wisconsin shore during July–September at sizes ranging from 20 to 70 mm (J.M. Dettmers, J. Janssen, and R.S. Fulford, unpublished data).

Lake Michigan is large enough to have significant currents (Beletsky et al. 1999). The lake also is large enough to have effects such as Ekman transport owing to the rotation of the earth, but the biological impact of these currents is mostly unstudied. Water currents in offshore areas of Lake Michigan during late summer have been measured at up to 55 $cm \cdot s^{-1}$, with a median value of 17 $cm \cdot s^{-1}$ (Pickett et al. 1983). Early studies on Lake Michigan water currents identified many areas of upwelling or downwelling along both western and eastern shorelines (Ayers et al. 1958). Taken together, these observations suggest that the hydrodynamics of Lake Michigan interact with the developmental ontogeny of yellow perch to produce an extended pelagic period that might distribute age-0 yellow perch far from where they were hatched. Such a phenomenon might affect basin-wide fluctuations in yellow perch recruitment success (Clapp and Dettmers 2004).

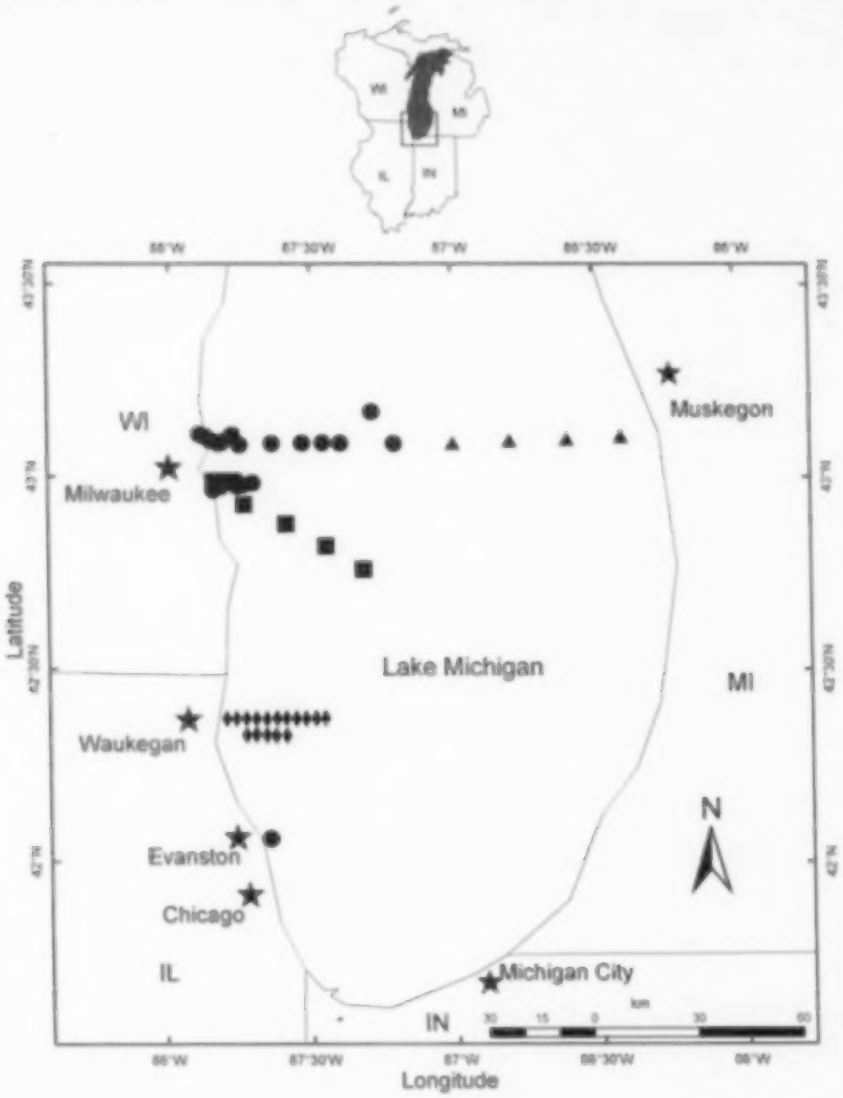
Owing to developing evidence that pelagic age-0 yellow perch are found well offshore and the limited understanding of how physical forces affect early life stages of yellow perch in Lake Michigan, we developed the following questions that required sampling across multiple scales. Is there evidence that yellow perch larvae are advected by water mass movements in Lake Michigan (small-scale sampling, ~1.6 km)? If yellow perch larvae are advected, how far offshore do they travel (mesoscale sampling, ~13 km, and cross-lake sampling, ~120 km)? Are larger (older) larvae found farther offshore (mesoscale sampling)? Is there a difference between nearshore and offshore food resources (mesoscale sampling)? Our work focuses on the first few weeks of life when fish will be most susceptible to hydrodynamic transport.

Methods

To address our hypotheses, we sampled larval and pelagic age-0 yellow perch in a variety of locations and years (Table 1; Fig. 1) using similar gear described below. Yellow perch were collected at night with 1 m × 2 m neuston nets towed horizontally just beneath the water surface between June and August in each year. Tows were conducted at speeds of 2–3 knots for lengths of time varying between 5 and 30 min, depending on the scale addressed (see below and Table 1). Mesh sizes of the neuston nets were varied depending on expected size of yellow perch larvae from 500 μm during

© 2005 NRC Canada

Fig. 1. Map of southern Lake Michigan showing sampling locations for early life stages of yellow perch (*Perca flavescens*): ●, sampling by Loyola University; ■, sampling by North Carolina State University; ▲, sampling by the University of Michigan; ◆, sampling by the Illinois Natural History Survey.



the first 2–3 weeks after hatching to 1000 µm by the end of June and 1800 µm thereafter, usually until the first week of August. A flowmeter mounted in the center of the mouth of the net allowed estimation of the volume of water filtered, which was used to calculate density of larvae. Samples were preserved in ethanol for later sorting and identification in the laboratory.

Small-scale sampling

To determine how upwelling and downwelling affected advection, two nearshore stations (within 1.6 km of shore) were selected based on water depth (Table 1). For purposes of comparison, the deeper station was considered offshore relative to the shallow station. At each station, three replicate surface neuston tows, each 5 min long, were taken once to twice each week, weather depending. Stations were located on the western side of Lake Michigan off Evanston, Illinois, in 1998, 1999, and 2000 and Milwaukee, Wisconsin, in 2001 and 2002 (Table 1; Fig. 1). There was no river plume near Evanston, but near Milwaukee, a substantial, usually warmer water plume discharges from the Milwaukee River via Milwaukee Harbor. To avoid this plume, which would alter larval yellow perch densities, we noted temperature and longshore current direction and visually checked color in the harbor as well as north and south of the harbor. We then sampled either north or south of Milwaukee Harbor to avoid the discharge. Data for determining the effect of upwelling events were analyzed as an analysis of covariance

© 2005 NRC Canada

(ANCOVA) with corrected relative offshore/nearshore abundance (100 × [(density offshore)/(density offshore + density inshore)]), henceforth "relative offshore percentage", as the dependent variable. Relative offshore percentage varies between 0 and 1.0 and was arcsine square root transformed for statistical analysis. The covariate was the difference between the shallow station surface temperature and the National Oceanic Atmospheric Administration midlake buoy surface temperature. A more extreme upwelling resulted in a more negative ΔT, whereas a more extreme downwelling generated a more positive ΔT. Location (Wisconsin versus Illinois) was a group variable; location and year are confounded. For each depth and date, we employed the mean density from the three samples.

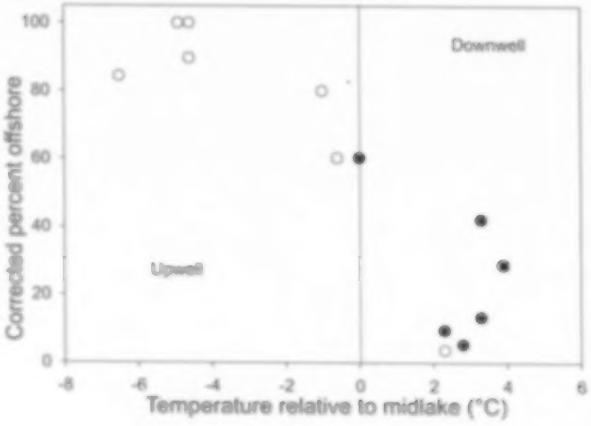
Mesoscale sampling

We interpret mesoscale to mean a bounded but sufficiently large area where hydrodynamics of the area are governed by oceanographic phenomena such as strong wind-driven currents and earth-spin that affect water movement at scales larger than upwelling/downwelling events (Beletsky et al. 2004). To investigate offshore transport at a mesoscale level, we sampled an east–west transect of about 12 km, roughly 1.5 km north of Waukegan Harbor, Illinois, between late May and early August during 2000–2002 (Table 1; Fig. 1). Five stations along the transect were selected for larval fish sampling at the following distances from shore: 1.8, 4.6, 7.4, 10.1, and 12.9 km. Larval fish sampling occurred approximately weekly, weather depending. In the laboratory, larval fishes were identified and counted and total lengths of up to 50 individuals from each tow were measured to the nearest 0.1 mm using an image analysis program. Length data for each year were analyzed using ANCOVA with week as the group variable and distance from shore as the covariate. We also examined the week × distance offshore interaction.

Additional mesoscale samples were taken on nine nights between 22 June and 31 July in 2001 using both a Tucker trawl and a neuston net and three nights between 17 and 30 June in 2002 off Milwaukee using a neuston net for comparison with the Waukegan samples taken by neuston net during the same time frame each year (Table 1; Fig. 1).

On the same nights as larval fish sampling, we collected epilimnetic (top 10 m of water) zooplankton samples at distances from shore of 1.8 and 12.9 km to compare the availability of food in nearshore versus offshore locations. At each station, two replicate vertical lifts were taken using a 0.5-m-diameter, 73-μm-mesh conical zooplankton net. The net was unmetered and we assumed 100% net efficiency when calculating zooplankton density. Although this assumption was not always valid, the data are still valid from a comparative perspective, given that changing conditions throughout the season affected our sampling in the same way on each sampling date and that our primary interest was comparing zooplankton abundance between nearshore and offshore locations. Samples were immediately preserved in 5% sugar formalin. In the laboratory, zooplankton were enumerated and identified into the following categories: cladocerans to genus, cyclopoid copepodites, calanoid copepodites, copepod nauplii, Macrothrididae spp., Sididae spp., and rotifers. Uncommon taxa were noted. For each sample, up to three 5-mL subsamples were taken from adjusted volumes that provided a count of at least 20 individuals of most taxa. Upon completion of each subsample, counting ceased for each taxon in which 100 individuals were additively counted. During the counting procedure, length measurements also were taken so that up to 20 individuals for each species and replicate were measured. Weekly zooplankton densities and lengths for each year were analyzed using a split-plot repeated-measures analysis of variance (Maceina et al. 1994) with density or length as the dependent variable and year, week, and sampling station (i.e., distance offshore) as class variables.

Fig. 2. Corrected percent offshore catch of yellow perch (*Perca flavescens*) in relation to offshore water temperature at two nearshore stations in southwestern Lake Michigan. Sampling occurred in Illinois (●) during 1998–2000 and in Wisconsin (○) during 2001–2002.



Cross-lake sampling

In 2002, we sampled across Lake Michigan on 26–28 June using neuston nets as described above to assess the distribution of yellow perch from the Illinois–Wisconsin side to the Michigan side. There were three segments to this sampling. A cross-lake sample consisted of two of these segments, with one segment being from Muskegon, Michigan, to about midlake and the second being from Milwaukee to about midlake (Table 1; Fig. 1); tows were 30 min. The cross-lake sampling was complemented with a third segment that included the mesoscale samples in Illinois to confirm very nearshore densities along the western side of the lake.

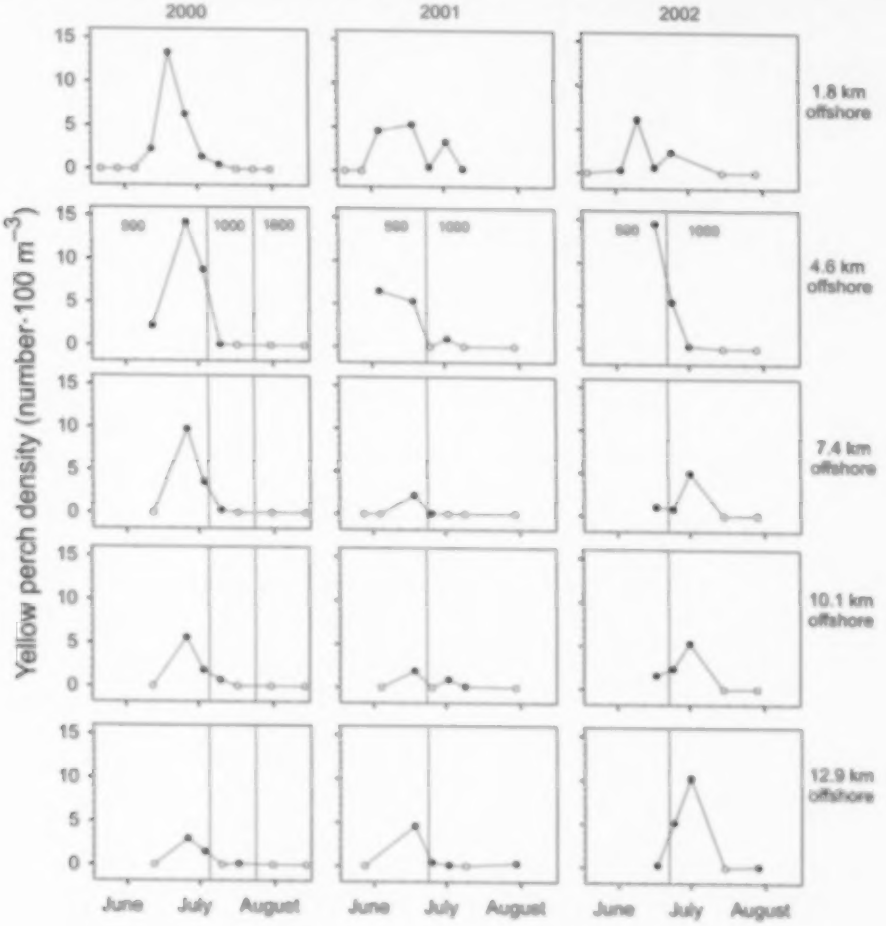
Results

Small-scale sampling

Only yolk-sac larvae were collected, ranging in density from 0 to 600·100 m^{-3}. Highest densities occurred at the nearshore station on the most extreme downwelling night (ΔT = 3.8 °C) at Evanston (57–600 larvae·100 m^{-3} for the three individual samples) and at the offshore station on the most extreme upwelling night (ΔT = –5 °C) at Milwaukee (177–228 larvae·100 m^{-3} for the three individual samples).

© 2005 NRC Canada

Fig. 3. Larval yellow perch (*Perca flavescens*) density collected along a 12-km-long nearshore–offshore transect near Waukegan Harbor, Illinois, with a 1 m × 2 m neuston net towed at the surface at night. ○, weeks when sampling occurred but no yellow perch larvae were collected; vertical lines, changes in mesh size of the neuston net.



ANCOVA revealed a strong negative relationship with ΔT ($F_{[1,10]} = 15.4$, $P < 0.003$) and no location effect ($F_{[1,10]} = 0.1$, $P > 0.5$). Hence, larval yellow perch were relatively more abundant at nearshore stations along the west shoreline for downwellings and at offshore stations for upwellings (Fig. 2). Several strong upwelling samples for Illinois are not included because there were no larval yellow perch in either the nearshore or the offshore sites. Presumably, the fish larvae were farther offshore than our offshore station on those sampling occasions.

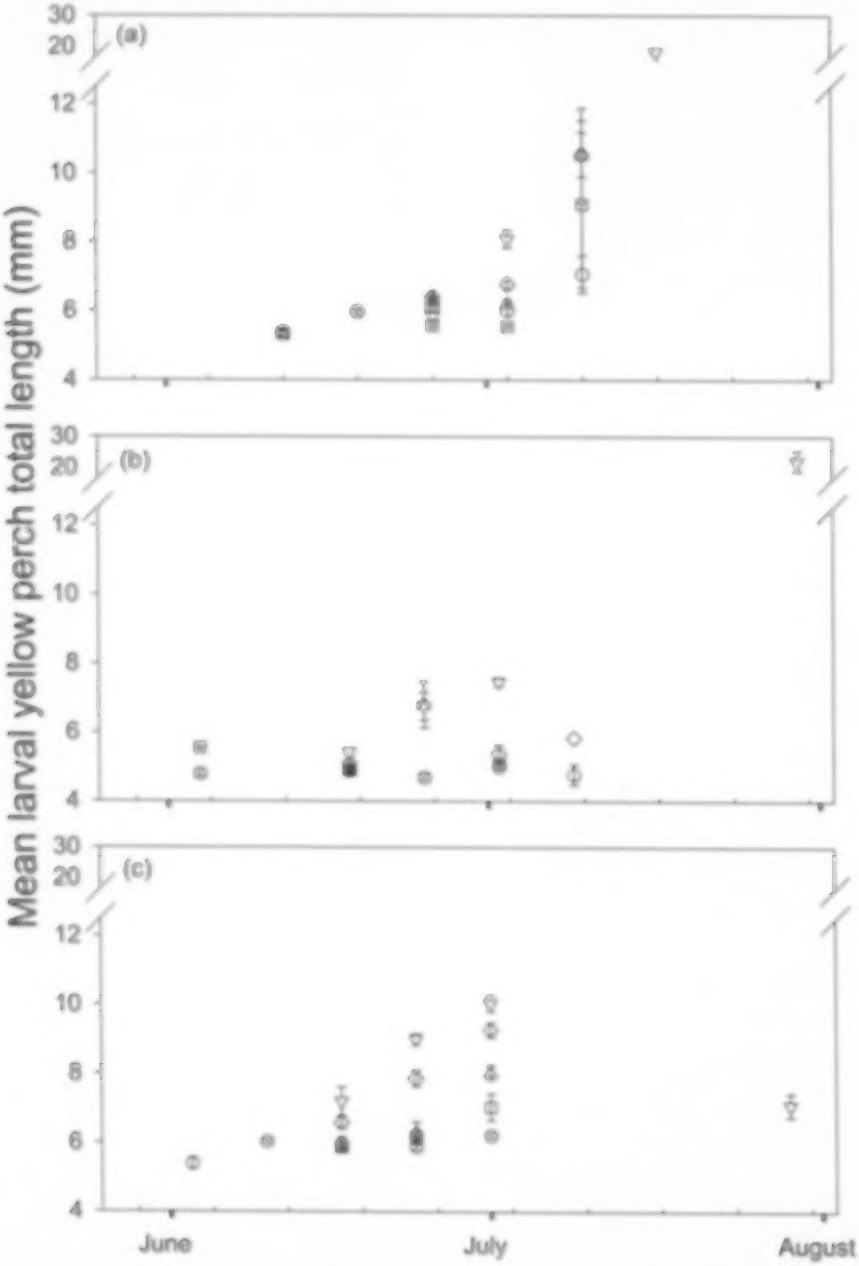
Mesoscale sampling

Primarily post-yolk sac larvae and age-0 yellow perch were collected during this phase of sampling. Larval yellow perch patterns of appearance were qualitatively similar for all years sampled (Fig. 3). Yellow perch larvae initially were collected closest to shore, but within 2 weeks, they were found at all sampling stations. Hatching continued for about 4 weeks, during which time yellow perch larvae were small regardless of distance from shore. Yellow perch larvae were detected at all sampling stations for several weeks but after mid-July were found only at our site farthest from shore (12.9 km). In 2000 and 2002, larval yellow perch densities were qualitatively similar but densities were much lower in 2001 (Fig. 3). In all years, the highest densities occurred at 4.6 km offshore, even under different density conditions (years).

Generally, size of yellow perch larvae increased through time within years and increased with distance from shore, but these patterns were complex in nature, with consistently significant interaction terms (Fig. 4). Newly hatched larvae were collected at our nearshore location 1.8 km from shore during a 5-week period each year (Fig. 4), indicating that this was the primary hatching location. These newly hatched larvae also were collected at sites well offshore, but only before the last week of June. After mid-June, size of yellow perch larvae collected increased in all years. Analysis of the patterns during late June though July revealed that yellow

© 2005 NRC Canada

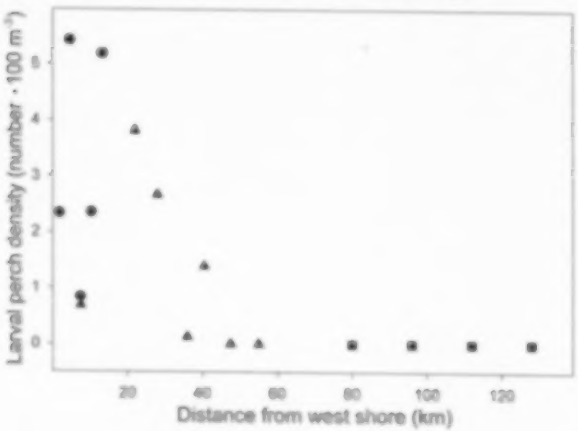
Fig. 4. Mean (±1 SE) total length of larval yellow perch (*Perca flavescens*) collected along a 12-km-long nearshore–offshore transect near Waukegan Harbor, Illinois, with a 1 m × 2 m neuston net towed at the surface at night during May–August (*a*) 2000, (*b*) 2001, and (*c*) 2002. ○, mean length at 1.8 km offshore; □, mean length at 4.6 km offshore; △, mean length at 7.4 km offshore; ◇, mean length at 10.1 km offshore; ▽, mean length at 12.9 km offshore.



perch grew with time ($F_{[1,700]}$ = 149.02, P < 0.0001) (Fig. 4*a*). Specifically, pelagic yellow perch were longer during the third week of July than in the second week of July; yellow perch larvae from both of these weeks were longer than larvae collected during late June and early July, which did not differ from each other (Tukey's multiple comparison, P < 0.05). Yellow perch length also increased with distance from shore in 2000 ($F_{[4,945]}$ = 97.01, P < 0.0001). During 2001, no significant growth patterns were detected for either time of year (P = 0.87) or distance from shore (P = 0.17), largely because yellow perch were not collected consistently across enough sites to allow for statistical differentiation (Fig. 4*b*). Mean yellow perch length did not differ through time in 2002 ($F_{[2,361]}$ = 1.61, P = 0.20) but did

© 2005 NRC Canada

Fig. 5. Density of yellow perch (*Perca flavescens*) larvae 2 weeks after peak hatching across the southern Lake Michigan basin from Waukegan, Illinois, to Muskegon, Michigan. Sampling was conducted during 26–28 June 2002 by the Illinois Natural History Survey (●, 1.8–13 km offshore), Loyola University (▲, 7.5–55 km offshore), and the University of Michigan (■, 80–128 km offshore). All sample densities are referenced as distances offshore from the west shore of Lake Michigan.



increase with increasing distance from shore ($F_{[1,361]}$ = 283.6, $P < 0.0001$) (Fig. 4c).

Comparison of Waukegan and Milwaukee samples from 2001 and 2002 revealed that larval yellow perch moved offshore along the entire western side of Lake Michigan, regardless of location in the southern basin of the lake. In 2001, larger yellow perch were collected farther from shore than smaller yellow perch (mean (±SD) length at 1.8 km offshore = 4.9 ± 0.5 mm, mean length at 12.9 km offshore = 7.2 ± 5.2 mm; $F_{[1,518]} = 4.21$, $P = 0.04$), with no effect of location (Waukegan versus Milwaukee: $F_{[1,518]} = 3.21$, $P = 0.08$). In 2002, the same pattern followed, with larger yellow perch collected farther from shore (mean length at 1.8 km offshore = 6.1 ± 0.4 mm, mean length at 12.9 km offshore = 9.2 ± 1.8 mm; $F_{[1,1146]} = 376.93$, $P < 0.0001$), again with no effect of location ($F_{[1,1146]} = 0.33$, $P = 0.57$).

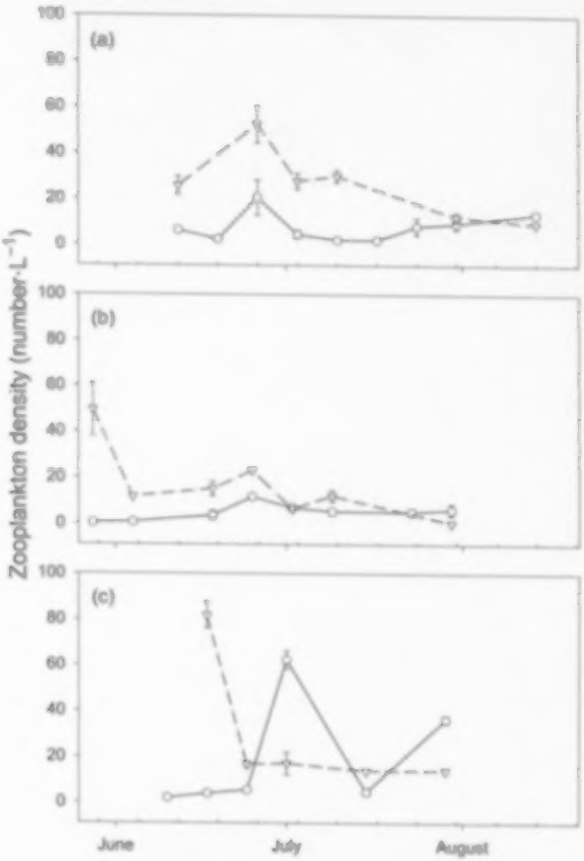
Cross-lake sampling

Yellow perch larvae were consistently found from the west shoreline to about 50 km offshore. They were not found farther offshore or closer to the eastern shore of the lake (Fig. 5), suggesting that the source of most larvae occurred along the western shore in 2002. At the time we sampled, about 2 weeks after the peak of hatching, yellow perch had not yet been transported completely across the lake.

Mesoscale zooplankton sampling

Crustacean zooplankton densities were initially higher offshore than nearshore across all years, but the difference decreased as the season progressed (Fig. 6). Statistically, zooplankton density was greater offshore ($F_{[1,12]} = 5.89$, $P = 0.03$) with no effect of year ($F_{[2,2]} = 3.25$, $P = 0.24$), no temporal trend within years ($F_{[8,12]} = 0.73$, $P = 0.66$), and no location × week interaction ($F_{[8,12]} = 1.45$, $P = 0.27$). Although mean crustacean zooplankton length also was

Fig. 6. Mean (±1 SE) weekly crustacean zooplankton density taken from the top 10 m of water at nearshore (○, 1.8 km offshore) and offshore (▽, 12.9 km offshore) locations near Waukegan Harbor, Illinois, during May–August of (*a*) 2000, (*b*) 2001, and (*c*) 2002.



greater offshore in all three years ($F_{[1,76]} = 10.03$, $P = 0.002$) (Fig. 7), patterns associated with zooplankton length were much more complex than for density. Crustacean zooplankton length differed among years ($F_{[2,2]} = 20.39$, $P = 0.05$), with mean zooplankton length in 2002 greater than in either 2000 or 2001 (Tukey's multiple comparison, $P < 0.05$). Furthermore, zooplankton length varied temporally but not consistently ($F_{[17,76]} = 2.88$, $P = 0.0008$), leading to a location × week interaction ($F_{[9,76]} = 3.52$, $P = 0.001$).

Discussion

Our results demonstrate that larval yellow perch are transported well offshore in Lake Michigan and that larger, pelagic age-0 yellow perch were found farther from shore. Based on analyses of larval yellow perch swimming ability, their distribution was unlikely to be influenced by swimming until after reaching at least 9.5 mm (Houde 1969). In our case, yellow perch were between 6 and 7 mm long when they first appeared 13 km offshore. Our small-scale results also indicate that larval yellow perch do not actively swim offshore, or if oriented to swim offshore, their swimming is

© 2005 NRC Canada

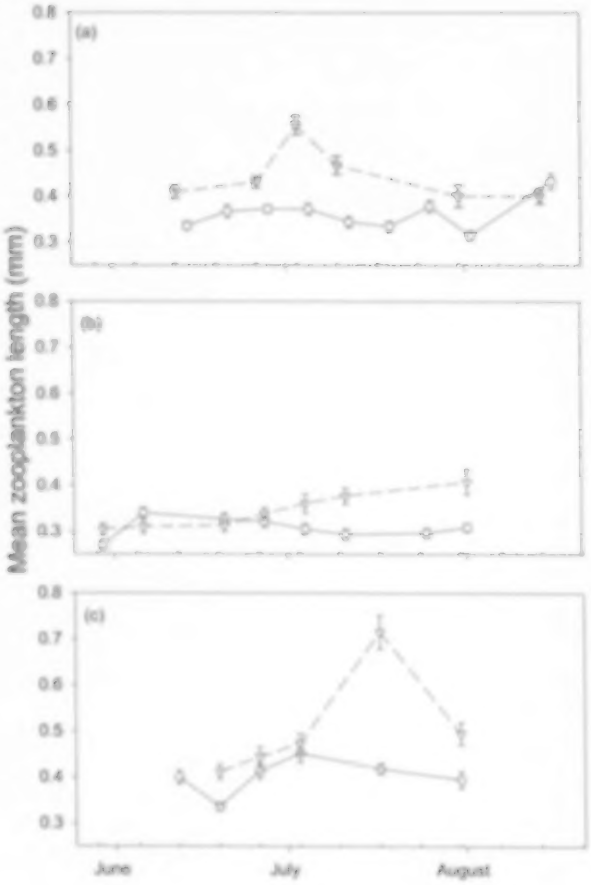


Fig. 7. Mean (±1 SE) length of crustacean zooplankton taken from the top 10 m of water at nearshore (○, 1.8 km offshore) and offshore (▽, 12.9 km offshore) locations near Waukegan Harbor, Illinois, during May–August of (*a*) 2000, (*b*) 2001, and (*c*) 2002.

not strong enough to counter an upwelling or downwelling (onshore) movement of water (Houde 1969). Consistent with this is the collection of large amounts of the epilithic green alga *Cladophora* at a station about 15 km east of Milwaukee on 24 June 2002. This sample had the highest density (17.5-100 m^{-3}) and largest yellow perch collected from Wisconsin stations that night (part of the mesoscale sampling). *Cladophora* is shed from the Wisconsin shallow rocky areas in June and the dying filaments drift, providing a marker for passive transport from nearshore areas.

The transport likely is a phenomenon of two interacting factors: the early life history of yellow perch and the hydrodynamics of a large, deep lake. In smaller and shallower lakes, *Perca* spp. larvae actively move offshore from the littoral zone where the eggs were deposited (Post and McQueen 1988; Urho 1996). Their initial swimming speed is slow, about 1 $cm \cdot s^{-1}$ (Houde 1969), relative to typical Lake Michigan coastal current speeds, which are commonly 10–20 $cm \cdot s^{-1}$ (Mortimer 1975; Sato 1975; Beletsky et al. 2004). Thus, for a pelagic larva, hydrodynamic transport is expected.

Our study confirms the basic principles outlined by Beletsky et al. (2004) for larval yellow perch drift. Their model estimated the drift of passive neutrally buoyant particles originating along the Illinois coast just north of Chicago using the meteorological conditions for 1998, 1999, and 2000. The model began on 1 June each year, approximately the time of yellow perch swimup, and was based on that of Beletsky and Schwab (2001), incorporating the Princeton ocean model (Blumberg and Mellor 1987). Environmental factors driving the model included wind stress, heat flux, free-slip lateral boundary conditions, and bottom friction. In general, particles moved offshore and circulated in a clockwise direction. Many particles were trapped in a southern Lake Michigan basin gyre, but some escaped to the northern basin via a northward coastal current along the eastern shore. Predicted dispersion by the end of June varied among years. In 2000, most particles were scattered between the middle of the lake and the eastern shore (to about Muskegon). Particles were most concentrated between the western shore (to just north of Milwaukee) and the middle of the lake in 1999 but widely dispersed throughout the entire southern basin in 1998. By the end of July of all three years, about the earliest time that age-0 yellow perch can appear in shallow water, particles were widely dispersed with a density bias toward the eastern shore and extending up that coast about one-third of its length.

Offshore transport may be a contributing mechanism for the genetic homogeneity of yellow perch in southern Lake Michigan, whereas yellow perch from Green Bay, a semi-isolated bay on the western shore with very limited mixing to the open lake, were genetically distinct (Miller 2003). The homogeneity means that there must be thorough mixing of yellow perch throughout the southern basin. Mixing apparently does not occur at the postdemersal stage; Horns (2001) found region-specific growth patterns that Janssen and Luebke (2004) related to differences in habitat and forage base. A long-term mark–recapture study found little evidence of substantial adult yellow perch movement and a large percentage of fish recaptured close to their initial capture location (D. Glover, Illinois Natural History Survey, 400 17th Street, Zion, IL 60099, USA, personal communication). With this lack of movement and recapture near original tagging locations, it is unlikely that mixing occurs in adults. Therefore, mixing must have occurred at the larval and juvenile stages.

Our cross-lake results, along with the hydrodynamic modeling of Beletsky et al. (2004), suggest that many, or even most, demersal yellow perch along the eastern coast may originate from spawning activity along the western coast. Yellow perch habitat preferences are consistent with this source–sink hypothesis. Adult yellow perch prefer rocky habitat, apparently both for foraging (Wells 1980; Janssen et al. 2005) and for spawning (Dorr 1982; Robillard and Marsden 2001); rocky habitat is the dominant feature along the western coast, whereas the eastern coast is primarily sandy (Powers and Robertson 1968; Janssen et al. 2005).

Passive transport of larval yellow perch in Lake Michigan means that young yellow perch have an early life history similar to that of marine coastal fishes imposed on them by

© 2005 NRC Canada

the hydrodynamics of a macroscopic lake system. An extended pelagic period is the typical habit for marine coastal fishes (Bonhomme and Planes 2000). When these fish larvae are pelagic, their survival is frequently determined by an interaction between physical and biological forcing factors. For instance, recruitment of northern anchovy (*Engraulis mordax*) is lower during windy and stormy conditions because appropriate food resources for first-feeding larvae are not available (Lasker 1975). On a more global scale, recruitment in Atlantic herring (*Clupea harengus*) is related, in part, to the North Atlantic Oscillation (Axenrot and Hansson 2003).

Consequently, recruitment of yellow perch in Lake Michigan may show patterns different from those of smaller lakes where recruitment is commonly influenced by nearshore predation on juveniles (Rudstam et al. 1996; Paxton and Winfield 2000). To better understand how larval fish transport may influence recruitment, we address three areas: offshore environment, duration offshore, and the return nearshore.

Offshore environment

The nearshore and offshore environments differ in their thermal regime, zooplankton abundance, and potential predators. Overall, the offshore environment offers a more stable thermal environment as the lake stratifies because the stratification is at first intermittent (Mortimer 2004) and easily disrupted by upwellings and downwellings, especially nearshore. Food resources also appear to be greater offshore. We saw greater zooplankton density offshore, a finding consistent with previous work (Hawkins and Evans 1979; Evans and Jude 1986). Upwelling can increase zooplankton abundance in patches offshore where eddies are generated (Megard et al. 1997). Larval yellow perch transported via upwelling may end up in areas of abundant food and reduced predation risk, much like larval capelin (*Mallotus villosus*) experience in marine systems (Leggett et al. 1984).

Offshore duration

Studies in smaller lakes suggest that yellow perch larvae generally spend 2–7 weeks in offshore areas (Whiteside et al. 1985; Wang and Eckmann 1994; Post et al. 1995). In southern Lake Michigan, the time spent offshore appears to be longer. Annual nearshore bottom trawl assessments by the Illinois Natural History Survey at a site near Waukegan during 1988–2002 showed that juveniles appear nearshore during August–September (J.M. Dettmers, unpublished data) some 10–16 weeks after hatching.

The long offshore duration in southern Lake Michigan may be related to pelagic food resources. Most work has suggested that nearshore movement occurs when larvae reach 25–30 mm (Whiteside et al. 1985; Post and McQueen 1988; Wu and Culver 1992). Once age-0 yellow perch become demersal, they experience an ontogenetic diet shift from zooplankton to benthic organisms (Whiteside et al. 1985; Post and McQueen 1988; Wu and Culver 1992). This shift may be related to the summer collapse in *Daphnia* populations (Mills and Forney 1981; Wu and Culver 1992; Wang and Eckmann 1994). For Lake Michigan, an explanation based on a *Daphnia* decline is unlikely because the peak in most crustacean zooplankton, including *Daphnia*, occurs in August and September (Torke 1975), at least 60 days after yellow perch have hatched and much longer than the 30–40 days typically ascribed to their early pelagic phase (Whiteside et al. 1985). Moreover, Cladocera in Lake Michigan are negligible in abundance until late July (Lehman and Caceres 1993) and are increasing at the time when yellow perch are expected to become demersal. Hence, there may be little energetic advantage for pelagic age-0 yellow perch to seek out benthic food resources, which typically reduce growth of age-0 yellow perch as compared with zooplankton (Prout et al. 1990). Instead, delaying the switch to benthic nursery areas may make sense when offshore zooplankton are relatively abundant and *Diporeia hoyi* availability is much reduced (Nalepa et al. 1998).

Return to shore

During the shift to demersal prey, juvenile yellow perch must move from the pelagic open-water environment to areas were they can feed on benthic organisms. In most cases, this movement would occur in two directions: horizontally (inshore) and (or) vertically (towards the bottom). Compared with studies in smaller systems where offshore sites are often only 1 km from shore (Wang and Eckmann 1994; Urho 1996; Anderson et al. 1998), Lake Michigan distances are much greater. We observed yellow perch larvae about 50 km offshore 2 weeks after the peak hatch in 2002. Because we have, as yet, only studied the early phase of offshore movement in any detail, we do not know how far yellow perch must swim or be transported to nearshore nursery grounds or the mechanism by which they return nearshore. Hydrodynamic predictions suggest wide dispersal such that some fish might have to move 60 km or more (Beletsky et al. 2004). Studies on other large-scale freshwater systems had sites up to 10 km from shore (Wu and Culver 1992; Post et al. 1995), but in both studies, water depth was much shallower (25 m, Post el al. 1995; 10 m, Wu and Culver 1992) than typical offshore sites in Lake Michigan (depth = 50–100 m). One study found larval *Perca fluviatilis* in water over 50 m deep, but this was less than 1 km from shore (Wang and Eckmann 1994).

Distances in smaller lakes are not great and an oriented swim by a juvenile in any direction will easily encounter the littoral zone. But based on hydrodynamic modeling of Lake Michigan (Beletsky et al. 2004), substantial numbers of juveniles will be tens of kilometres offshore at a size when, in smaller lakes, they are expected to become demersal. Some age-0 yellow perch were found at 50–75 m, along with juveniles of deepwater sculpin (*Myoxocephalus thompsoni*) and bloater (*Coregonus hoyi*) (Geffen and Nash 1992). Modeling also demonstrates that some age-0 yellow perch should encounter shallow water if they do not orient toward shore on their own (Beletsky et al. 2004).

Nonetheless, some age-0 fish may never make it to shore or end up in very poor habitat. Yellow perch about 3–5 cm were reported from 25 m deep in late August 1990 at Julian's Reef (Edsall et al. 1993), which is 13 km from the west shore and surrounded by water about 50 m deep. Adult yellow perch have never been reported from this area and it is likely that these yellow perch would grow very slowly, be eaten, or die if they did not leave. Yellow perch have been identified in stomachs of lake trout (*Salvelinus namaycush*)

© 2005 NRC Canada

collected at Sheboygan Reef (C. Madenjian, US Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan, personal communication), which is well offshore and has a minimum depth of about 40 m.

The relatively long pelagic period of Lake Michigan yellow perch may be a consequence of the long distances transported. The scale of the transport, with fish larvae as far as 50 km offshore about 2 weeks after hatching, far exceeds the typical offshore distance that fish would encounter in most yellow perch lakes. There is growing evidence that marine coastal fishes, which typically have long pelagic periods (Bonhomme and Planes 2000), have behavioral methods of returning to shore (Armsworth et al. 2001); however, the brief evolutionary history of yellow perch in Lake Michigan (<10 000 years) makes it unlikely that a fish evolved in smaller lakes will have such behaviors.

The negative relationship between alewife (*Alosa pseudoharengus*) and yellow perch (Shroyer and McComish 2000), exacerbated by zebra mussels (*Dreissena polymorpha*) (Janssen and Luebke 2004), suggests that yellow perch recruitment is not affected by juveniles failing to return from offshore. The inverse relationship between yellow perch recruitment and zooplankton abundance (Dettmers et al. 2003) is consistent with the pattern of depression of zooplankton by both the invasive alewife and zebra mussel. In such a case, rapid offshore transport to areas of higher zooplankton abundance should be favorable to yellow perch recruitment. This is especially true in the face of reduced abundance of the energy-rich deepwater amphipod *Diporeia*, which was an important component of age-0 yellow perch diets in Lake Michigan (Wells 1980; D. Jude, unpublished data), but which now are absent from their diets (Pothoven et al. 2000). Hence, loss of *Diporeia* from a large area of eastern Lake Michigan (Nalepa et al. 1998) that might be the hydrodynamically favored endpoint of drift from the west side could increase basin-wide mortality of yellow perch. In this case, we expect that fish production from the eastern shore should be substantially diminished compared with historical values and less than that from the western shore. Offshore transport of yellow perch larvae, in conjunction with changes to the food web mediated by invasive species, can help to explain the extended period of poor yellow perch recruitment in Lake Michigan.

Acknowledgements

We thank W. Brofka, B. Brylawski, S. Hensler, P. Hirethota, A. Jaeger, M. Luebke, S. Miehls, A. Spencer, J. Thompson, and K. Wolfe for their dedication and help in both the field and the laboratory and K. Stainbrook and L. Page for help with figures. We also thank the vessel crews of the RV *Blue Heron*, RV *Neeskay*, and RV *Cyclops* and the Wisconsin Department of Natural Resources for providing vessel time. Comments from two anonymous reviewers substantially improved the paper. Funding was provided in part by the Great Lakes Fishery Trust, Illinois–Indiana Sea Grant, Michigan Sea Grant, Wisconsin Sea Grant award No. NA86RG0047, the Federal Aid in Sport Fish Restoration Program, Project F-123-R, administered by the Illinois Department of Natural Resources, and the Illinois Natural History Survey.

References

Anderson, M.R., Fisher, S.J., and Willis, D.W. 1998. Relationship between larval and juvenile yellow perch abundance in eastern South Dakota glacial lakes. N. Am. J. Fish. Manag. **18**: 989–991.

Armsworth, P.R., James, M.K., and Bode, L. 2001. When to press on or turn back: dispersal strategies for reef fish larvae. Am. Nat. **157**: 434–450.

Axenrot, T., and Hansson, S. 2003. Predicting herring recruitment from young-of-the-year densities, spawning stock, and climate. Limnol. Oceanogr. **48**: 1716–1720.

Ayers, J.C., Chandler, D.C., Lauff, G.H., Powers, C.F., and Henson, E.B. 1958. Currents and water masses of Lake Michigan. Gt. Lakes Res. Inst. Publ. No. 3.

Beletsky, D., and Schwab, D.J. 2001. Modeling circulation and thermal structure in Lake Michigan: annual cycle and interannual variability. J. Geophys. Res. **106**: 19745–19771.

Beletsky, D., Saylor, J.H., and Schwab, D.J. 1999. Mean circulation in the Great Lakes. J. Gt. Lakes Res. **25**: 78–93.

Beletsky, D., Schwab, D.J., Mason, D.M., Rutherford, E., McCormick, M.J., Vanderploeg, H.A., and Janssen, J. 2004. Modeling the transport of larval yellow perch in Lake Michigan. *In* Estuarine and Coastal Modelling, 8th International Conference, 3–5 November 2003, Monterey, Calif. American Society of Civil Engineers, Reston, Virginia. pp. 439–454.

Blumberg, A.F., and Mellor, G.L. 1987. A description of a three-dimensional coastal ocean circulation model. *In* Three dimensional ocean models, coastal and estuarine sciences, 5. *Edited by* N.S. Heaps. American Geophysical Union, Washington, D.C. pp. 1–16.

Bonhomme, F., and Planes, S. 2000. Some evolutionary arguments about what maintains the pelagic interval in reef fishes. Environ. Biol. Fishes, **59**: 365–383.

Brandt, S., Mason, D., MacNeill, D., Coates, T., and Gannon, J. 1987. Predation by alewives on larvae of yellow perch in Lake Ontario. Trans. Am. Fish. Soc. **116**: 641–645.

Clady, M., and Hutchinson, B. 1975. Effect of high winds on eggs of yellow perch, *Perca flavescens*, in Oneida Lake, New York. Trans. Am. Fish. Soc. **104**: 524–525.

Clapp, D.F., and Dettmers, J.M. 2004. Yellow perch research and management in Lake Michigan: evaluating progress in a cooperative effort, 1997–2001. Fisheries, **29**(11): 11–19.

Dettmers, J.M., Raffenberg, M.J., and Weis, A.K. 2003. Exploring zooplankton changes in southern Lake Michigan: implications for yellow perch recruitment. J. Gt. Lakes Res. **29**: 355–364.

Dorr, J.A. 1982. Substrate and other environmental factors in reproduction of the yellow perch (*Perca flavescens*). Ph.D. thesis, University of Michigan, Ann Arbor, Mich.

Edsall, T.A., Kennedy, G.W., and Horns, W.H. 1993. Distribution, abundance, and resting microhabitat of burbot on Julian's Reef, southwestern Lake Michigan. Trans. Am. Fish. Soc. **122**: 560–574.

Evans, M.S., and Jude, D.J. 1986. Recent shifts in *Daphnia* community structure in southeastern Lake Michigan, USA: a comparison of the inshore and offshore regions. Limnol. Oceanogr. **31**: 56–67.

Geffen, A.J., and Nash, R.D.M. 1992. The life-history of deepwater sculpin, *Myoxocephalus thompsoni* (Girard), in Lake Michigan: dispersal and settlement patterns during the first year of life. J. Fish Biol. **41**(Suppl. B): 101–110.

Hartman, K.J., and Margraf, F.J. 1993. Evidence of predatory control of yellow perch (*Perca flavescens*) recruitment in Lake Erie, USA. J. Fish Biol. **43**: 109–119.

Hawkins, B.E., and Evans, M.S. 1979. Seasonal cycles of zooplankton biomass in southeastern Lake Michigan. J. Gt. Lakes Res. **5**: 256–263.

© 2005 NRC Canada

Henderson, B.A., and Nepszy, S.J. 1985. Recruitment of yellow perch *Perca flavescens* affected by stock size and water temperature in lakes Erie and St. Clair 1965–85. J. Gt. Lakes Res. **14**: 205–215.

Heyer, C.J., Miller, T.J., Binkowski, F.P., Calderone, E.M., and Rice, J.A. 2001. Maternal effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*). Can. J. Fish. Aquat. Sci. **58**: 1477–1487.

Horns, W.H. 2001. Spatial and temporal variation in length-at-age and condition of yellow perch in southern Lake Michigan during 1986–1988. N. Am. J. Fish. Manag. **21**: 580–591.

Houde, E.D. 1969. Sustained swimming ability of larvae of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*). J. Fish. Res. Board Can. **26**: 1647–1659.

Houde, E.D. 1994. Differences between marine and freshwater fish larvae: implications for recruitment. ICES J. Mar. Sci. **51**: 91–97.

Janssen, J., and Luebke, M.A. 2004. Preference for rocky habitat by age-0 yellow perch and alewife. J. Gt. Lakes Res. **30**: 93–99.

Janssen, J., Berg, M., and Lozano, S. 2005. Submerged terra incognita: the abundant but unknown rocky zones. *In* State of Lake Michigan: ecology, health and management. *Edited by* T. Edsall and M. Munawar. Academic Publishing, Amsterdam, Netherlands. pp. 113–139.

Johnson, B.M., Luecke, C., Stewart, R.S., Staggs, M.D., Gilbert, S.J., and Kitchell, J.F. 1992. Forecasting effects of harvest regulations and stocking of walleyes on prey fish communities in Lake Mendota, Wisconsin. N. Am. J. Fish. Manag. **12**: 797–807.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. **73**: 453–462.

Leggett, W.C., Frank, K.T., and Carscadden, J.E. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. **41**: 1193–1201.

Lehman, J.T., and Caceres, C.E. 1993. Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. Limnol. Oceanogr. **38**: 879–892.

Maceina, M.J., Bettoli, P.W., and DeVries, D.R. 1994. Use of a split-plot analysis of variance design for repeated-measures fishery data. Fisheries, **19**(3): 14–20.

Marsden, J.E., and Robillard, S.R. 2004. Decline of yellow perch in southwestern Lake Michigan, 1987–1997. N. Am. J. Fish. Manag. **24**: 952–966.

Megard, R.O., Kuns, M.M., Whiteside, M.C., and Downing, J.A. 1997. Spatial distributions of zooplankton during coastal upwelling in western Lake Superior. Limnol. Oceanogr. **42**: 827–840.

Miller, L.M. 2003. Microsatellite DNA loci reveal genetic structure of yellow perch in Lake Michigan. Trans. Am. Fish. Soc. **132**: 503–513.

Mills, E.L., and Forney, J.L. 1981. Energetics, food consumption, and growth of young yellow perch in Oneida Lake, New York. Trans. Am. Fish. Soc. **110**: 479–488.

Mortimer, C.H. 1975. Physical characteristics of Lake Michigan and its responses to applied forces. Argonne National Laboratory, Argonne, Ill.

Mortimer, C.H. 2004. Lake Michigan in motion. University of Wisconsin Press, Madison, Wis..

Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A., and Lozano, S.J. 1998. Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993. Can. J. Fish. Aquat. Sci. **55**: 2402–2413.

Nash, R.D.M., and Geffen, A.J. 1988. Spatial and temporal changes in the offshore larval fish assemblage in southern Lake Michigan. J. Gt. Lakes Res. **17**: 25–32.

Nielsen, L.A. 1980. Effect of walleye *Stizostedion vitreum vitreum* predation on juvenile mortality and recruitment of yellow perch *Perca flavescens* in Oneida Lake, New York, USA. Can. J. Fish. Aquat. Sci. **37**: 11–19.

Paxton, C.G.M., and Winfield, I.J. 2000. Population dynamics of underyearling coarse fish. Environment Agency (U.K.) R&D Rep. Ref. No. W222. Environment Agency, Bristol, England.

Pickett, R.L., Campbell, J.E., Clites, A.H., and Partridge, R.M. 1983. Satellite-tracked current drifters in Lake Michigan. J. Gt. Lakes Res. **9**: 106–108.

Post, J.R., and McQueen, D.J. 1988. Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): a response to prey or predators? Can. J. Fish. Aquat. Sci. **45**: 1820–1826.

Post, J.R., Rudstam, L.G., and Schael, D.M. 1995. Temporal and spatial distribution of pelagic age-0 fish in Lake Mendota, Wisconsin. Trans. Am. Fish. Soc. **124**: 84–93.

Pothoven, S.A., Nalepa, T.F., and Brandt, S.B. 2000. Age-0 and age-1 yellow perch diet in southeastern Lake Michigan. J. Gt. Lakes Res. **26**: 235–239.

Powers, C.F., and Robertson, A. 1968. Subdivisions of the benthic environment of the upper Great Lakes, with emphasis on Lake Michigan. J. Fish. Res. Board Can. **25**: 1181–1197.

Prout, M.W., Mills, E.L., and Forney, J.L. 1990. Diet, growth, and potential competitive interactions between age-0 white perch and yellow perch in Oneida Lake, New York, U.S.A. Trans. Am. Fish. Soc. **119**: 966–975.

Robillard, S.R., and Marsden, J.E. 2001. Spawning substrate preference of yellow perch along a sand–cobble shoreline on southwestern Lake Michigan. N. Am. J. Fish. Manag. **21**: 208–215.

Rudstam, L.G., Green, D.M., Forney, J.L., Stang, D.L., and Evans, J.T. 1996. Evidence of interactions between walleye and yellow perch in New York State lakes. Ann. Zool. Fenn. **33**: 443–449.

Sato, G.K. 1975. Lake currents and temperatures near the western shore of Lake Michigan. Ph.D. thesis, University of Wisconsin-Milwaukee, Milwaukee, Wis.

Shroyer, S.M., and McComish, T.S. 2000. Relationship between alewife abundance and yellow perch recruitment in southern Lake Michigan. N. Am. J. Fish. Manag. **20**: 220–225.

Torke, B.G. 1975. The population dynamics and life histories of crustacean zooplankton at a deep-water station in Lake Michigan. Ph.D. thesis, University of Wisconsin-Milwaukee, Milwaukee, Wis.

Urho, L. 1996. Habitat shifts of perch larvae as survival strategy. Ann. Zool. Fenn. **33**: 329–340.

Wang, N., and Eckmann, R. 1994. Distribution of perch (*Perca fluviatilis* L.) during their first year of life in Lake Constance. Hydrobiologia, **277**: 135–143.

Wells, L. 1980. Food of alewives, yellow perch, spottail shiners, trout-perch, and slimy and fourhorn sculpins in southeastern Lake Michigan. US Fish Wildl. Service. Tech. Pap. No. 98.

Whiteside, M.C., Swindoll, C.M., and Doolittle, W.L. 1985. Factors affecting the early life history of yellow perch, *Perca flavescens*. Environ. Biol. Fishes, **12**: 47–56.

Wu, L., and Culver, D.A. 1992. Ontogenetic diet shift in Lake Erie age-0 yellow perch (*Perca flavescens*): a size-related response to zooplankton density. Can. J. Fish. Aquat. Sci. **49**: 1932–1937.

© 2005 NRC Canada

The relative influence of breeding competition and habitat quality on female reproductive success in lacustrine brook trout (*Salvelinus fontinalis*)

Paul J. Blanchfield and Mark S. Ridgway

Abstract: Egg losses for female salmonines primarily occur through competition for egg incubation sites (i.e., redds) and the differences in quality among these sites. Through detailed observations and an experiment linking egg survival to groundwater flow, we estimated the relative influence of redd superimposition and habitat quality on female reproductive success for a population of lake-spawning brook trout (*Salvelinus fontinalis*). Three quarters of all spawning sites were reused by multiple females; however, brood loss was much less (28%–38%) because large females spawned earlier and constructed deeper nests. The relationship between groundwater flow rate and egg survival was not linear, with consistent egg survival occurring only at sites with flows over 20 mL·m^{-2}·min^{-1}. Varying scenarios of redd superimposition and habitat-related egg survival resulted in an estimated 4%–21% of deposited eggs surviving to emergence and greatly reduced the size-related advantages of larger females owing to fecundity. Limited numbers of high-quality spawning sites and overall low survival of eggs resulted in habitat being the dominant route of egg loss. In the absence of female competition, spawning habitat alone accounted for egg losses of 67%–91% and points to the importance of physical habitat features in the maintenance of brook trout populations.

Résumé : Les pertes d'oeufs chez les femelles des salmoninés se produisent à cause de la compétition pour les sites d'incubation des oeufs (i.e. nids) et des différences de qualité de ces sites. Des observations détaillées et une expérience mettant en relation la survie des oeufs et l'écoulement des eaux souterraines nous ont permis d'estimer l'importance relative de la superposition des nids et de la qualité de l'habitat sur le succès reproductif des femelles dans une population d'ombles de fontaine (*Salvelinus fontinalis*) qui se reproduisent en lac. Trois-quart de tous les sites de ponte sont utilisés successivement par plusieurs femelles; cependant, les pertes des masses d'oeufs sont moins importantes (28–38 %) parce que les grosses femelles pondent plus tôt et construisent des nids plus profonds. La relation entre le taux d'écoulement de l'eau phréatique et la survie des oeufs n'est pas linéaire et il ne se produit de survie uniforme des oeufs qu'au sites ayant un écoulement supérieur à 20 mL·m^{-2}·min^{-1}. Divers scénarios de superposition des nids et de survie des oeufs en fonction de la qualité de l'habitat nous amènent à estimer que 4–21 % des oeufs pondus survivent jusqu'à l'émergence, ce qui réduit considérablement les avantages reliés à la taille chez les grosses femelles à fécondité plus élevée. Les nombres limités de sites de ponte de grande qualité et la survie globale faible des oeufs ont comme conséquence que l'habitat est la cause principale de la perte des oeufs. En l'absence de compétition entre les femelles, l'habitat de ponte à lui seul explique 67–91 % des pertes d'oeufs, ce qui démontre l'importance des caractéristiques de l'habitat physique dans le maintien des populations d'ombles de fontaine.

[Traduit par la Rédaction]

Introduction

The theoretical limit of reproductive success in female salmonines is defined by the power function relating fecundity to body size. Achieving this limit is compromised by competition among females for access to spawning sites and differences in the physical characteristics of spawning sites. Competition among females for spawning sites can be intense and superimposed redds (sequential use of a spawning site by more than one female salmonine) can limit reproductive success and recruitment (McNeil 1964; Essington et al. 2000; Hendry et al. 2001). Spawning site quality is largely defined by substrate composition and particle size, as well as water depth and flow (Reiser and Wesche 1977; Crisp and

Received 15 October 2004. Accepted 29 June 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 27 October 2005.
J18358

P.J. Blanchfield.[1,2] Department of Biology, York University, 4700 Keele St., Toronto, ON M3J 1P3, Canada, and Harkness Laboratory of Fisheries Research, Ontario Ministry of Natural Resources, Aquatic Ecosystem Science Section, 3rd Floor North, 300 Water St., Peterborough, ON K9J 8M5, Canada.
M.S. Ridgway. Harkness Laboratory of Fisheries Research, Ontario Ministry of Natural Resources, Aquatic Ecosystem Science Section, 3rd Floor North, 300 Water St., Peterborough, ON K9J 8M5, Canada.

[1]Corresponding author (e-mail: BlanchfieldP@dfo-mpo.gc.ca).
[2]Present address: Fisheries and Oceans Canada, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.

 doi: 10.1139/F05-176 © 2005 NRC Canada

Carling 1989; Bjorn and Reiser 1991). These physical features singly or in combination directly affect embryo survival in many salmonines (Chapman 1988). As a result of these factors, embryo survival can be low (16%–32%, McNeil 1966; 7%–20%, Godin 1982; Bradford 1995) and clearly below the limits defined by the relationship between body size and fecundity.

Observations of redd superimposition point to spawning site selection based on certain characteristics of habitat and highlight the possibility that spawning habitat is generally a limiting resource in this group of fishes. Certainly, observations associating specific habitat features (the trinity of water depth, flow, and substrate particle size) with redd distribution in the field are common (e.g., Hoopes 1972; Knapp and Vredenburg 1996) and support the idea that production of age-0 fish is a function of the supply of spawning habitat (Knapp et al. 1998). Despite the apparent linkage between spawning habitat characteristics and redd distribution, only recently have models of physical spawning habitat successfully predicted use in the field (Knapp and Preisler 1999; Geist 2000; Geist et al. 2000).

Some have cautioned against assuming that body size alone is a strong measure of reproductive success in this group of fishes because of the potential for reproductive success to be affected by competition among females and spawning habitat quality (Holtby and Healey 1986; McPhee and Quinn 1998). In one study on coho salmon (*Oncorhynchus kisutch*), redd superimposition accounted for greater losses of egg biomass than did habitat quality, with larger females losing proportionately less of their reproductive investment relative to smaller females (van den Berghe and Gross 1989). The exponential relationship between female size and egg biomass in the coho study was lowered as a result of the effects of both competition and habitat quality (gravel size and interstitial area for egg survival) but the general pattern remained unchanged; large females clearly had a reproductive advantage over smaller females in a manner similar to the power function relating fecundity to female body size (van den Berghe and Gross 1989).

The mating system of brook trout (*Salvelinus fontinalis*) in lakes provides a unique opportunity to quantify the influence of female reuse of spawning sites and habitat quality on the survival of young. Female brook trout compete for access to spawning sites where upwelling groundwater is present (Blanchfield and Ridgway 1997). The importance of groundwater for maintaining brook trout populations has been known for some time (Latta 1965), and in lakes, the presence of groundwater flow is thought to be the primary criterion for the selection of spawning sites by females (Fraser 1982; Curry and Noakes 1995; Blanchfield and Ridgway 1997). The flow of groundwater at spawning sites increases the survival from egg to emergence by providing a stable environment and removing metabolic wastes from developing embryos (Sowden and Power 1985; Curry et al. 1995). Groundwater sites also shorten the time required for development to a free-swimming stage because groundwater is generally warmer than ambient water temperatures during the incubation period (Embody 1934).

In this study, we extend our previous observations of a brook trout mating system (Blanchfield and Ridgway 1997, 1999; Blanchfield et al. 2003) to examine the key factors limiting female reproductive success in a lake population. Extensive reuse of spawning sites, as well as rapid replacement of females during removal experiments, indicate that spawning sites can be limiting (Blanchfield and Ridgway 1997). The spatial distribution of spawning is highly skewed, with half of all spawning activity occurring at fewer than 20% of sites used (Blanchfield and Ridgway 1997). Breeding observations over 4 years have demonstrated that repeated use of specific redd sites is related to the rate of groundwater flow, with spawning activity occurring every year only at sites with higher seepage rates (Ridgway and Blanchfield 1998). The objective of this study was to determine the relative influence of female competition (redd superimposition) and habitat quality (groundwater seepage rate) on reproductive success of female brook trout. Reproductive success of females was not directly observed in the field but inferred when data on redd site use by females, female fecundity, and egg survival as a function of groundwater flow rate were combined. We chose this model approach for assessing reproductive success for two reasons. First, it allowed us to scope the range of egg survival based on variation in factors such as redd depth as a function of female size and egg survival as a function of groundwater flow. Second, the breeding adult population in Scott Lake is small (~70–190 individuals; Blanchfield and Ridgway 1997), so direct estimates of offspring production could potentially disrupt a relatively large proportion of adult spawners as well as a new cohort of brook trout. We also use these data to model, at the population level, the overall production of young after partitioning the main sources of egg mortality under natural breeding conditions.

Materials and methods

Study site

Scott Lake is a small, deep headwater lake (27.6 ha; maximum depth 25 m) located within Algonquin Park, Ontario (45°29′N, 78°43′W). The fish community is composed of *Culea inconstans*, *Pimephales promelas*, and *Phoxinus* spp. in addition to brook trout. The location of the spawning area and description of the site are provided in earlier publications (Blanchfield and Ridgway 1997; Ridgway and Blanchfield 1998; Blanchfield et al. 2003). The spawning area is somewhat more dispersed and individual redd sites are more distinct than observed in other brook trout lakes (Fraser 1985; Ridgway and Blanchfield 1998). The total spawning area is 829 m^2 and consists of six adjacent areas, each with a concentration of redds, with an overall redd density of 5.7 redds·100 m^{-2}.

Observations of female reproductive activity

Brook trout were captured and tagged in the middorsal area with t-tags, as well as numbered vinyl disk tags, to facilitate individual recognition of fish (see Blanchfield and Ridgway (1997) for details). Fish were initially captured using a 1.5-m trap net just prior to spawning (early October) and later with dip nets used by swimmers (with mask and snorkel) after spawning began. Fish were anaesthetized with tricainemethane sulfonate (MS 222) prior to tagging and fork length (millimetres) and weight (grams) for each fish were recorded. Most females in the spawning population

© 2005 NRC Canada

were marked (~80%) and their reproductive activities were documented on a daily basis during the breeding seasons. For fish that were not captured, or lost their tag during the breeding season, we estimated fork length (to within 5 cm) based on the size of other marked individuals that were in close proximity.

To monitor reproductive activities, we conducted a census of the spawning area four times daily (weather permitting) once spawning activity commenced (10 October in each year) until fish were no longer present on the spawning grounds (6 December 1994) or the lake surface was frozen (24 November 1995). During each census, the position of each female within the spawning area and its tag number were recorded on underwater slates by swimmers. Females were recorded as being on a redd site and spawning based on behavioural criteria. These criteria included digging behaviour for redd construction, guarding the redd from intrusion by other females before or after spawning, covering behaviour in which the female uses her caudal fin to cover the eggs deposited in the redd, and spawning behaviour (Blanchfield and Ridgway 1999). Collectively, these behaviours were interpreted as evidence of spawning at a particular redd site.

Redd superimposition and brood loss

Estimates of brood loss through redd superimposition were based on the depth of redds and the overlap that occurs in the construction of subsequent redds. The difference between the edge (unexcavated) and deepest part of an excavated redd in relation to the top of the water column was determined for 23 spawnings, each at a unique spawning site and by a different female (Steen and Quinn 1999). A regression of redd depth on female body size (fork length) was used to predict the egg burial depth of all females.

We recorded the number of spawnings that occurred at a specific site, the order in which they occurred, and the size of each female. Other studies that estimated the number of eggs sequentially deposited by females in a series of nests showed that there was reduction in eggs deposited in the last redds relative to egg deposition in the first redd (Maekawa and Hino 1990; Fleming 1996). We were unable to count the number of eggs deposited at each spawning, so we assumed that eggs were distributed equally among spawning events for females that spawned multiple times. Few data exist to resolve this assumption. In Atlantic salmon (*Salmo salar*), only marginal declines in the number of eggs deposited per nest were observed for females spawning in their first three redds (Fleming 1996). Female brook trout in Scott Lake spawn, on average, 2.7 times during the breeding season (Blanchfield and Ridgway 1997), so we have assumed that this does not result in declines in eggs per nest with each spawning. The redd depth criterion was used to determine whether the eggs deposited during individual spawning events were completely lost owing to multiple use of a single site by different females (van den Berghe and Gross 1989). Because we were not able to measure the size of every spawning female at Scott Lake, and therefore had to estimate size for some fish, we took two approaches to model egg loss owing to site reuse. We assumed a complete loss of one brood to superimposition for every spawning by later-spawning females that were (*i*) larger or equal in size than earlier-spawning females and (*ii*) larger, equal, or <5 cm smaller in size than earlier-spawning females. Thus, only female size and corresponding digging depth were used to model egg losses owing to superimposed redds.

Estimates of habitat quality

Habitat quality in this study was the groundwater seepage rate at redd sites. Measurements of groundwater flow at spawning sites, as well as randomly chosen sites within the spawning area, were made prior to the start of the 1994, 1995, and 1996 breeding seasons using seepage meters (Blanchfield and Ridgway 1996, 1997; Ridgway and Blanchfield 1998). We included flow rates from 1996 to increase our sample size from which to model groundwater flow at sites that we did not measure in previous years. We used the mean rate of groundwater flow from all 3 years combined in our estimation of habitat quality because flow rate did not differ among years for 14 sites measured annually (repeated-measures analysis of variance: $F = 0.69$, $p = 0.51$). Based on the mean rates of groundwater flow at spawning and random sites within the breeding area ($n = 53$), an inverse distance weighting (IDW) interpolation method was used to predict rates of groundwater flow for all spawning sites ($n = 92$; Ridgway and Blanchfield 1998). IDW interpolation determines cell values using a linearly weighted combination of a set of sample points (ArcView software; Environmental Systems Research Institute 1992). By this method, an interpolated 1-m resolution raster grid of groundwater flow values was produced for the entire spawning area. The average of cell values within 1 m of each spawning site (i.e., the surrounding eight cells) was then calculated as the groundwater flow at that site.

Egg survival experiment

To determine the effect of groundwater flow (i.e., habitat quality) on egg survival at Scott Lake, we conducted an experiment using egg hatchboxes (Whitlock-Vibert; described in Garrett and Bennett 1996) during the 1997 breeding season. We measured groundwater flow using seepage meters (described above) at nine previously used spawning sites and at one random site located close (<2 m) to other spawning sites. We made separate crosses of the eggs of three ripe females (37.4–41.1 cm fork length) using two males, all anaesthetized lightly with MS 222. Eggs were incubated overnight in the lake, and the following day, 100 living eggs were placed in each hatchbox. Three hatchboxes, each containing 100 eggs of a different female, were buried in each of the spawning sites (~10 cm depth) and a mesh cover was placed over the buried egg boxes to prevent any disturbance from site reuse by spawning females. There were not equal numbers of eggs available from all females; thus, each set of three boxes did not always contain eggs from all three females ($n = 2$), and one box contained only 57 eggs (not included in analysis). Egg survival did not differ among females for the eight sites in which the eggs of all three females were present (analysis of variance: $F = 0.35$, $p = 0.71$). Egg boxes were left for a period of 88 days prior to retrieval, at which point the eggs were counted and scored as to survival and developmental stage. We considered missing

© 2005 NRC Canada

eggs as young that had emerged only if there were yolk sac fry (i.e., the stage just prior to emergence) present (alive or dead) in the hatchboxes. Egg survival was equal to the number of eggs alive in addition to the number of emerged young relative to the total number of eggs placed in the hatchboxes at the start of the experiment. Temperature was recorded hourly (Ryan TempMentors™, Ryan Instruments, Redmond, Washington) at six of the buried egg boxes to determine lake water temperatures during the incubation period.

Determination of female reproductive success

We did not sample the Scott Lake population to acquire a size–fecundity relationship because of the low numbers of adult females (~50–60 adult females; Quinn et al. 1994; Blanchfield and Ridgway 1997). Instead, we relied on the fecundity relationship of Vladykov (1956) ($Y = 30.487 \exp(0.01X)$, where Y is the number of eggs and X is female fork length in millimetres) to estimate egg numbers for female brook trout of different size. The additional question of egg size and survival has been addressed in other studies but was not part of this analysis.

Loss of eggs was inferred in the following way. Numbers of eggs deposited in redds was based on female size and the assumption of equivalent egg deposition per spawning for individual females that spawned multiple times. Our daily coverage of the spawning area captured whether or not female brook trout spawned at more than one site and if they spawned repeatedly at a single site (Blanchfield and Ridgway 1997). After accounting for egg loss owing to superimposition, the proportion of remaining eggs assumed surviving as a function of habitat quality (i.e., groundwater seepage rate) was determined based on the inferred flow of groundwater at spawning sites derived from the IDW model and the results from the egg survival experiment. Tag loss during the spawning season, late arrival of females onto the spawning grounds, and some breeding at night prevented an exact estimate of reproductive success for all females (Blanchfield and Ridgway 1997). A subset of females retained their individual tags throughout the spawning season and allowed us to estimate reproductive success for individuals of different size. Reproductive success was estimated for 31 females in 1994 (66% of all tagged females) and 29 females in 1995 (62% of all tagged females), which represents over half of the total estimated female spawning population in both years.

Population-level loss of eggs

Swimming the entire spawning area of Scott Lake four times daily over periods of 57 days (1994) and 45 days (1995) provided an opportunity to model the distribution of eggs among redds in a fully sampled mating system, that is, a mating system in which all spawning sites are known, as well as their frequency of use and the approximate size of females spawning in those sites. Population-level patterns of egg deposition and loss owing to habitat quality were based on two kinds of data. First, the distribution of seepage rates at all sites was derived from observed measurements using seepage meters and inferred values from the IDW model. Second, daily surveys of the spawning area and all redd sites provided data for mapping female spawning on redds and the estimated number of eggs deposited in redds based on female size. The behavioural criteria described above for assigning spawning activities were also used in the spawning area survey. Egg loss was inferred at each redd based on the relationship between groundwater seepage rate and egg survival in the hatchbox experiment. Female identity was based on observed tags or previous sightings based on location, body size, and markings. In this mating system, not all females are active on a given day and the number spawning was always a subset of the female population (Blanchfield and Ridgway 1997).

Results

Seasonal timing of spawning, redd depth, and frequency of redd site reuse

The range in body size of spawning female brook trout was approximately 25 cm in both years (1994: 26.5–51.5 cm fork length; 1995: 26.5–51.9 cm fork length). Daily monitoring of the breeding activities at Scott Lake revealed that the size of spawning female brook trout decreased throughout each breeding season (1994: $F_{[1,161]} = 114.2$, $R^2 = 0.41$, $p < 0.001$; 1995: $F_{[1,175]} = 16.2$, $R^2 = 0.09$, $p < 0.001$) (Fig. 1). The residence time of large females (>40 cm fork length) on the spawning area is approximately 10–20 days (Blanchfield and Ridgway 1997) and therefore, the seasonal decline in size of spawning females represents a slow turnover in females as the season progresses. The depth at which female brook trout buried their eggs increased with body size ($Y = -0.97 + 0.23X$, where Y is nest depth and X is female fork length in centimetres; $F_{[1,21]} = 6.0$, $R^2 = 0.22$, $p = 0.022$) such that the largest females constructed redds that were, on average, twice the depth of redds of the smallest females in this population (Fig. 2). Overall, there was extensive reuse of redd sites in this mating system with spawning by multiple females occurring at roughly three quarters of redd sites (78% and 72% in 1994 and 1995, respectively) (Fig. 3). More than half of all redd sites were used by three or more spawning females. Owing to the earlier breeding by larger females and the positive relationship between nest depth and female body size (Fig. 2), the extensive reuse of sites resulted in a smaller fraction of brood loss stemming from superimposition. Nest destruction owing to superimposition was estimated at 28% (1994) and 30% (1995) of all spawnings that occurred during the two breeding seasons if later-spawning females at a given site were of equal or greater fork length. Our alternate estimate, in which we allowed for additional brood loss by later-spawning females that were smaller (by <5 cm) than earlier-spawning females, resulted in a greater incidence of nest destruction (38% for both breeding seasons).

Egg emergence experiment

After 88 days, little or no emergence occurred from redds with groundwater flows less than or equal to 20 $mL \cdot m^{-2} \cdot min^{-1}$ (Fig. 4*a*). Eggs that were buried at redds with flow rates above 20 $mL \cdot m^{-2} \cdot min^{-1}$ showed increasing emergence with flow rate. The proportion of brook trout embryos that emerged from within the buried hatchboxes reached a maxi-

© 2005 NRC Canada

Fig. 1. Daily mean size of spawning female brook trout (*Salvelinus fontinalis*) during the (*a*) 1994 and (*b*) 1995 breeding seasons.

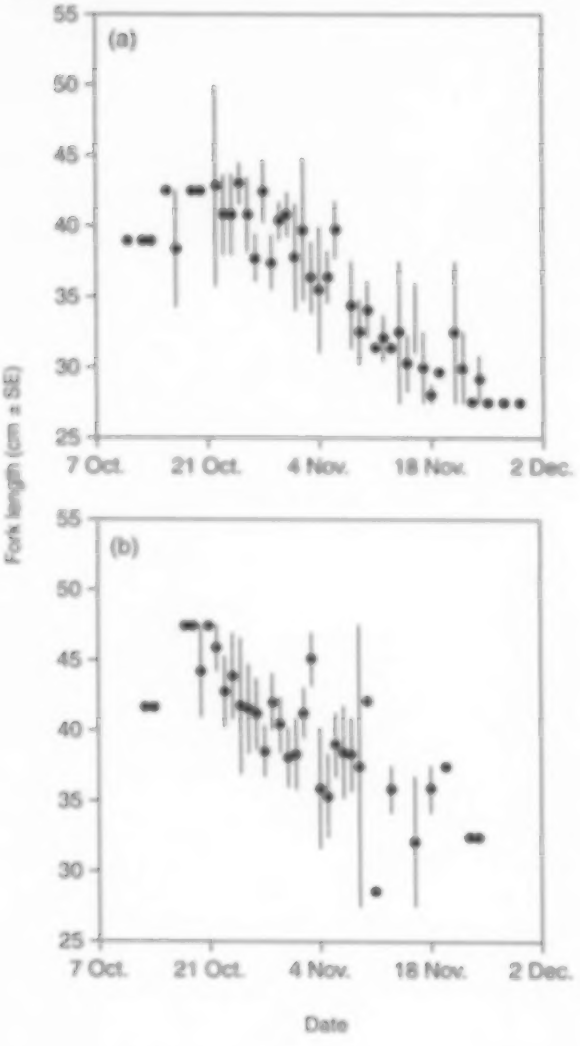
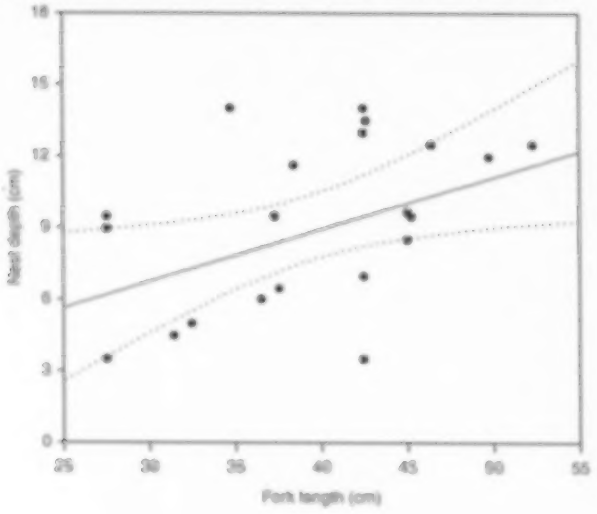


Fig. 2. Relationship between female body size and nest depth (solid line; $Y = -0.97 + 0.23X$) with 95% confidence intervals (dotted lines) for Scott Lake brook trout (*Salvelinus fontinalis*).



mum of 0.28 at the highest flow rate (~35 mL·m^{-2}·min^{-1}) (Fig. 4*a*).

The survival of eggs was also related to groundwater flow rates in redds. Survival of eggs at low flow rates was very low or nonexistent, while survival at flow rates equaling or exceeding 20 mL·m^{-2}·min^{-1} was consistent and did not increase with increasing groundwater flow rate (Fig. 4*b*). Comparing the patterns of emergence and survival as a function of groundwater flow rate points to the role of water temperature as a factor in affecting developmental timing and survival. For eggs that were buried at sites with a flow rate of approximately 20 mL·m^{-2}·min^{-1}, emergence after 88 days was low (Fig. 4*a*), but survival of brook trout embryos was similar to hatchboxes located at redds with higher flow rates (Fig. 4*b*). For brook trout embryos to emerge after 88 days, the mean daily temperature in the egg pockets would have to have been 5.6 °C (Embody 1934) ($Y = 183.16 \exp(-0.132X)$, where Y is days to emergence and X is temperature). Mean lake water temperature at redd sites during the incubation period was 3.4 °C (range: 1.8–7.1 °C), suggesting that groundwater was at least several degrees warmer than lake water during the incubation period. For redd sites with groundwater flow above 20 mL·m^{-2}·min^{-1}, mean survival was relatively constant at 37% (95% confidence interval CI: 28%–46%). The overall egg to alevin survival at the nine sites in which we had previously observed brook trout spawning was 20% (95% CI: 12%–29%).

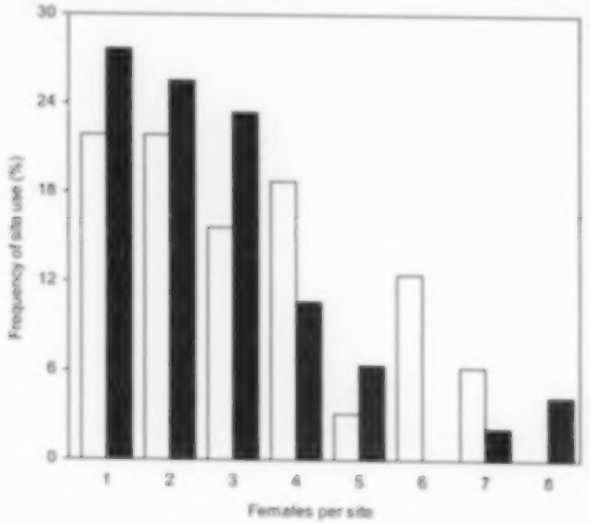
Female reproductive success

The results from the egg survival experiment were used to model the egg losses at redd sites with different seepage rates (Fig. 4*b*). Because territory quality was not continuous, we classified spawning sites based on the rate of groundwater flow. Sites of low quality (<11.2 mL·m^{-2}·min^{-1}) were classified as having no survival (0) (Fig. 4*b*, line section *i*). We assigned all sites with groundwater flow equaling or exceeding 20.6 mL·m^{-2}·min^{-1} an egg survival rate of 0.366, the mean from observed data (Fig. 4*b*, line section *ii*). We used three different scenarios to model egg survival as a function of groundwater flow for sites of groundwater flow between 11.2 and 20.6 mL·m^{-2}·min^{-1} (Fig. 4*b*). We inferred maximum egg survival (scenario A), a linear relationship ($Y = -0.484 + 0.043X$, where X is groundwater flow in mL·m^{-2}·min^{-1}) (scenario B), and minimum egg survival (scenario C) (Fig. 4*b*). Together, these scenarios provided a range of modeled egg survival for spawning sites with intermediate rates of groundwater flow (Fig. 4*b*).

The power function relating fecundity to female body size represents the theoretical limit of reproductive success for females of different size. Subsequently, egg loss resulting from superimposed redds reduced fecundity and accounted

© 2005 NRC Canada

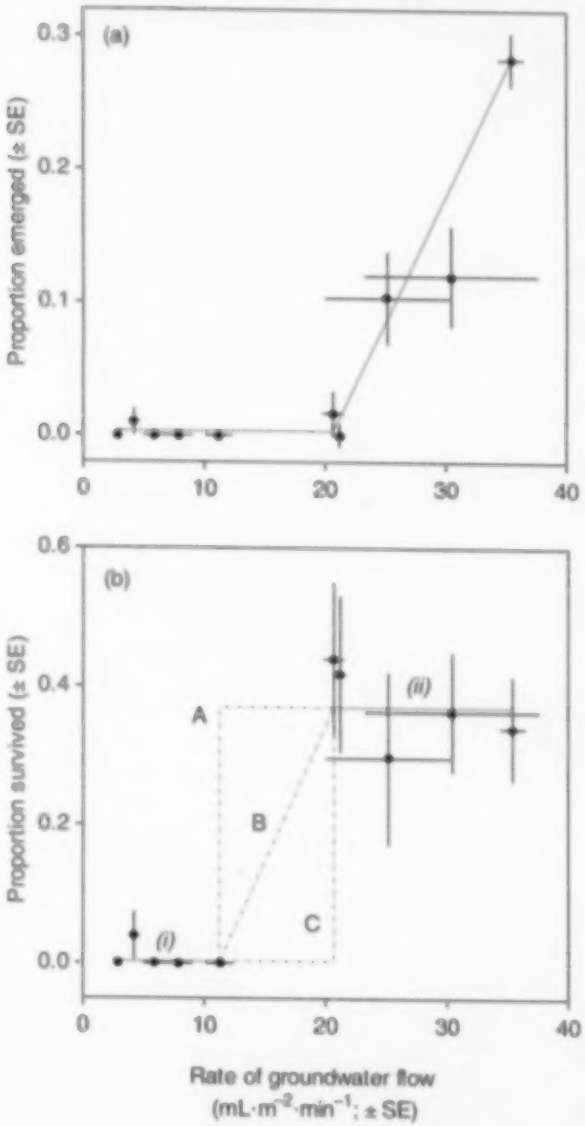
Fig. 3. Frequency of spawning site use by female brook trout (*Salvelinus fontinalis*) for the 1994 breeding season (open bars) and 1995 breeding season (solid bars).



for mean losses of 34% (95% CI: 19%–50%) and 27% (95% CI: 14%–41%) of eggs deposited in the 1994 and 1995 breeding seasons, respectively, assuming that spawning females lost one brood to every later-spawning female of equal or greater fork length at a given site (Figs. 5*a* and 5*b*). Deposited eggs that survived site reuse by females suffered further mean egg losses of 68%–93% depending on the scenario used to describe the relationship between egg survival and habitat quality (i.e., groundwater flow rate). Mean egg survival for female brook trout after accounting for losses to superimposition and habitat quality ranged from 6% to 21% (1994: scenario A, 21%, 95% CI: 15%–27%; scenario B, 12%, 95% CI: 8%–16%; scenario C, 6%, 95% CI: 2%–11%; 1995: scenario A, 21%, 95% CI: 16%–27%; scenario B, 11%, 95% CI: 7%–16%; scenario C, 6%, 95% CI: 1%–11%) (Figs. 5*a* and 5*b*).

Loosening our criterion to also include nest destruction by later-spawning females that were less than 5 cm smaller in fork length than earlier-spawning females increased our estimate of egg loss owing to superimposition by less than 10% (1994: 43%, 95% CI: 28%–59%; 1995: 33%, 95% CI: 20%–47%) (Figs. 5*c* and 5*d*). The additional egg loss from superimposition owing to relaxing our body size criterion was slightly greater in 1994 (9%) than in 1995 (6%). However, the exponential relationship between female size and number of eggs remaining after losses through nest destruction was similar in 1994 (Figs. 5*a* and 5*c*) because most additional egg loss was incurred by medium-sized females (n = 7; range: 31.4–42.3 cm fork length). In contrast, the additional egg loss owing to superimposition that occurred in the 1995 breeding season was limited to much larger females, including the largest females in this population (n = 5; range: 44.5–51.9 cm fork length). As a result, the relationship between female size and number of eggs surviving nest destruction was markedly lower between these two scenarios of brood loss in 1995 (Figs. 5*b* and 5*d*). Overall, the greater

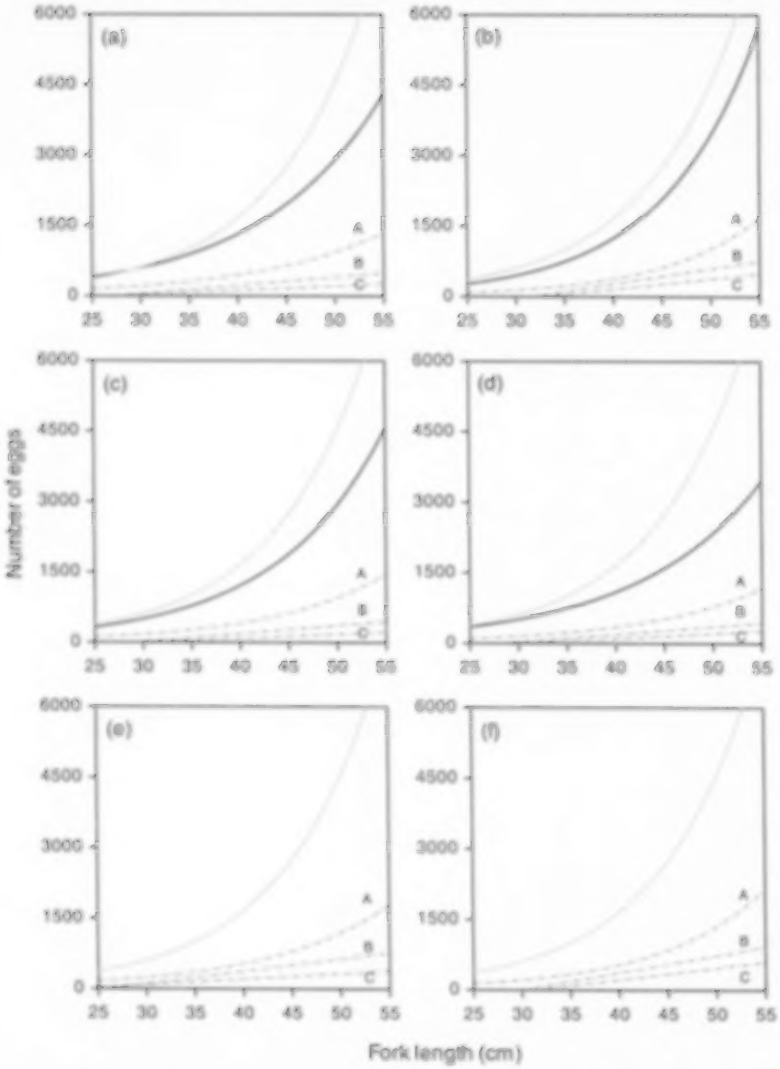
Fig. 4. Influence of groundwater flow on the (*a*) proportion of emerged fry and (*b*) egg survival for eggs held in hatchboxes and buried at brook trout (*Salvelinus fontinalis*) spawning sites. Each point is the mean of three hatchboxes per site, each containing the eggs of a different female (see text for exceptions). Egg survival was estimated to be (*i*) 0 when groundwater flow was <11.2 mL·m^{-2}·min^{-1} and (*ii*) constant at 0.366 at groundwater flows >20.6 mL·m^{-2}·min^{-1}. Three scenarios (A, B, and C) described egg survival as a function of groundwater flow for spawning sites between 11.2 and 20.6 mL·m^{-2}·min^{-1}. Scenario B is a linear relationship (Y = –0.4361 + 0.0389X).



egg loss owing to superimposed redds by smaller females made little difference in mean egg survival to emergence once egg loss owing to spawning habitat quality was included, 4%–19% (1994: scenario A, 18%, 95% CI: 12%–

© 2005 NRC Canada

Fig. 5. Number of eggs per spawning female brook trout (*Salvelinus fontinalis*) (top line in all panels) in relation to body size determined from Vladykov (1956). Modeled estimates of the number of eggs surviving after accounting for egg loss through brood superimposition (solid line) and the combined loss of eggs through superimposition and territory quality (scenarios A, B, and C in Fig. 4*b*) (broken lines) are shown in relation to female body size (1994: $n = 31$; 1995: $n = 29$). Egg loss through superimposition by later-spawning females of equal or greater size and subsequent loss to habitat quality scenarios is shown for (*a*) 1994 and (*b*) 1995. Egg loss through superimposition by later-spawning females of larger, equal, or smaller (by <5 cm) size with the combined loss to habitat quality is shown for (*c*) 1994 and (*d*) 1995. Egg loss owing solely to habitat quality scenarios is shown for (*e*) 1994 and (*f*) 1995. Fecundity and the modeled number of remaining eggs after losses to superimposition and combined egg loss to superimposition and habitat quality scenario A were best described by exponential relationships. The numbers of eggs remaining after combined losses to superimposition and habitat quality scenarios B and C were best fit with a linear model.



23%; scenario B, 9%, 95% CI: 6%–13%; scenario C, 4%, 95% CI: 1%–8%; 1995: scenario A, 19%, 95% CI: 14%–25%; scenario B, 10%, 95% CI: 6%–14%; scenario C, 5%, 95% CI: 0%–9%) (Figs. 5*c* and 5*d*).

In the absence of nest destruction from female competition, modeled outcomes of egg loss owing solely to habitat quality resulted in reductions of 67%–91% of egg numbers from the relationship between body size and fecundity for female brook trout (Figs. 5*e* and 5*f*). Modeled egg survival was 33% (95% CI: 30%–37%), 21% (95% CI: 16%–25%), and 13% (95% CI: 7%–19%) in 1994 for habitat quality scenarios A, B, and C, respectively (Fig. 5*e*). Similar levels of egg survival after accounting for losses owing solely to habitat quality were estimated for females during the 1995 breeding season (scenario A, 31%, 95% CI: 27%–35%; scenario B, 17%, 95% CI: 12%–22%; scenario C, 9%, 95% CI: 3%–15%) (Fig. 5*f*). We examined the relationship between female body size and the groundwater flow at sites chosen

© 2005 NRC Canada

for egg deposition. For each female, we chose the site of greatest flow where eggs were deposited because female brook trout can spawn at multiple sites. There were no size-related patterns in choice of sites by habitat quality (Spearman rank correlation: 1994, $r_s = -0.033$, $p = 0.86$, $n = 31$; 1995, $r_s = 0.23$, $p = 0.23$, $n = 29$).

After partitioning the major sources of egg loss in our scenarios, habitat quality reduced the potential reproductive output of female brook trout by 1.5–3.4 times that of redd superimposition through female competition for spawning sites. The difference in the mean percentage of modeled egg loss through the combined effects of female competition and habitat quality (Figs. 5*a*–5*d*) and that from habitat quality alone (Figs. 5*e* and 5*f*) ranged from 3% to 16% and became increasingly diminished as estimates of habitat quality worsened (range in mean differences pooled for year and level of superimposition: scenario A, 10%–15%; scenario B, 6%–11%; scenario C, 3%–8%).

Population-level egg loss

Spawning habitat quality, modeled by groundwater seepage rate, appeared to have the strongest effect on egg survival, and therefore, we estimated the losses of eggs at the population level as a function of groundwater seepage rate based on observations of spawning at all redd sites. Survival estimates associated with different redds were based on the approach used in estimating survival of eggs outlined above when determining the reproductive success of females of different size (Fig. 4*b*, scenarios A, B, and C).

The observed distribution of eggs deposited among redds in both years matched the frequency distribution of redds of different seepage rates (Kolmogorov–Smirnov test: 1994, $D_{0.05,14} = 0.36$, $p > 0.05$; 1995, $D_{0.05,14} = 0.29$, $p > 0.05$) (Fig. 6). Thus, spawning habitat use by females, as reflected in projected egg deposition (Figs. 6*c* and 6*d*), matched habitat availability at the population level (Figs. 6*a* and 6*b*). However, modeled differences in survival resulting from site differences in seepage rates reduced the total number of eggs available for production with full loss occurring at seepage rates below 11.6 $mL \cdot m^{-2} \cdot min^{-1}$ for all scenarios of habitat quality (Figs. 6*e* and 6*f*). The projected percent loss of total eggs deposited at or below this seepage rate was 14% of eggs in 1994 and 13% of eggs in 1995. Redds below this threshold represent 27% of all spawning sites observed in Scott Lake. At the threshold of 20.6 $mL \cdot m^{-2} \cdot min^{-1}$ and above this rate of groundwater flow, redds provide a consistent survival rate of 0.366 for all habitat quality scenarios (Figs. 6*e* and 6*f*). This category of redds was the least common in Scott Lake (20%) but provided between 36% and 100% of surviving eggs depending on habitat quality (1994 and 1995: scenario A, 36%–48%; scenario B, 59%–73%; scenario C, 100%) (Figs. 6*e* and 6*f*). The balance of egg production for the 1994 and 1995 cohorts appears to be derived from redd sites representing a transition from sites that provide no survival to sites that provide consistent survival (11.2–20.6 $mL \cdot m^{-2} \cdot min^{-1}$). These redd sites represent 53% of all redds used for egg deposition and produced 0%–64% of surviving eggs. At the population level, habitat quality resulted in a 68%–89% reduction in egg survival for Scott Lake brook trout (1994 and 1995: scenario A, 68%–69%; scenario B, 79%–81%; scenario C, 85%–89%) (Figs. 6*e* and 6*f*).

Discussion

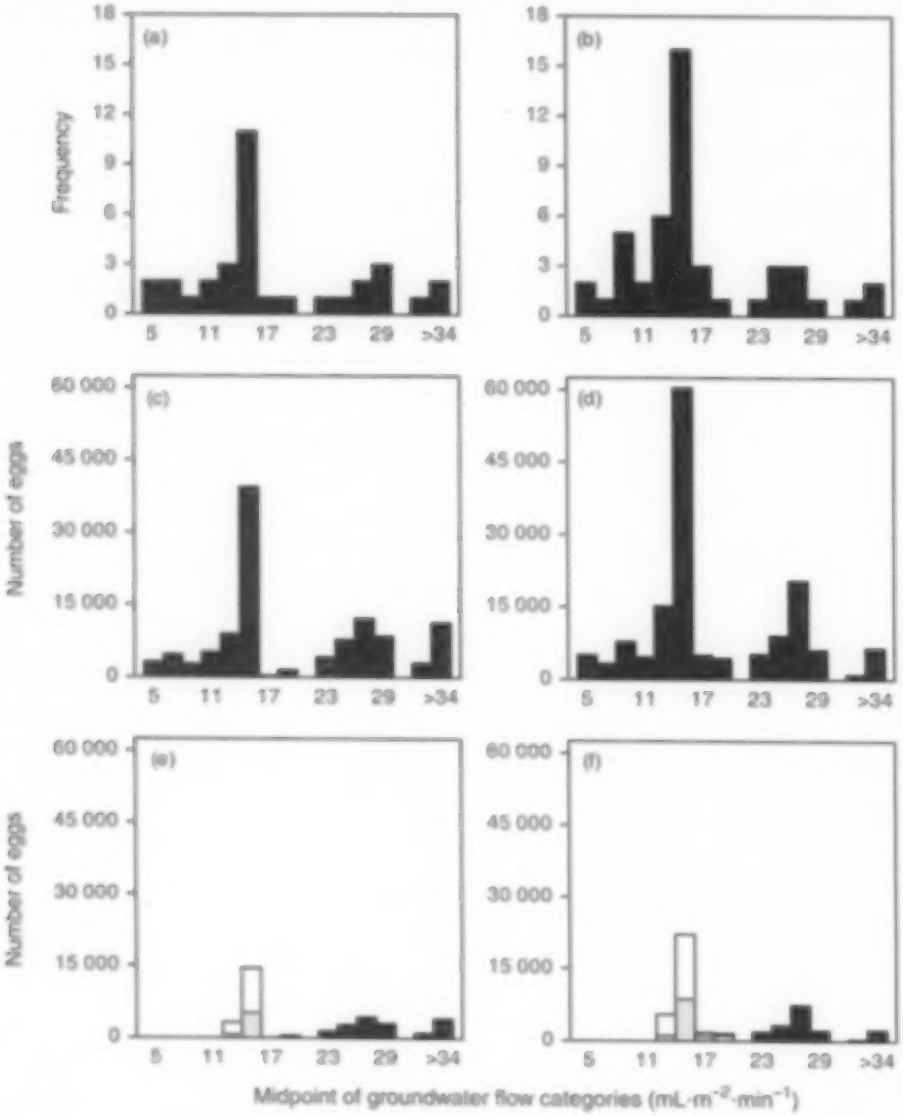
Habitat quality, measured as groundwater seepage rate, had a stronger influence on the reproductive success of female brook trout than competition for spawning sites. Egg incubation experiments clearly indicated a threshold effect of groundwater seepage rate on the emergence and survival of young brook trout. The fecundity of lake-spawning brook trout as a function of size was greatly reduced when the effects of both habitat quality and redd superimposition were modeled. However, habitat quality alone resulted in such significant egg mortality that larger female brook trout, because of their greater fecundity, retained only a slight relative advantage in effective or operational fecundity over smaller females. Our model of changes in the effective fecundity of female brook trout stemming from competition and site quality points to the importance of physical habitat in the maintenance of brook trout populations.

Ranking competition for redds ahead of habitat quality appears to be the general outcome of most salmonine studies examining the relationship between spawner abundance and offspring production (e.g., Fukushima et al. 1998; Essington et al. 2000). For example, reproductive success in coho salmon appears to be controlled primarily by competition for spawning sites and only secondarily by redd habitat quality (van den Berghe and Gross 1989). In coho salmon, redd superimposition lowers but does not fundamentally alter the power function from the theoretical limit of female reproductive success (Fig. 7 in van den Berghe and Gross 1989). In contrast, the power function relating fecundity to body size for lake-spawning brook trout is essentially flattened as a result of habitat quality differences among redd sites. The difference in the relative strength of the site quality – site competition dichotomy in determining egg survival may reflect a gradient in the strength of density-dependent mortality during the egg stage in salmonine mating systems. In many salmonine mating systems such as Pacific salmon, redd superimposition in large, dense populations of spawning fish likely represents a significant source of density-dependent mortality for eggs as female competition for sites increases with spawning population size. Pacific salmon appear to adjust their seasonal timing of reproduction to minimize egg loss under these conditions (Morbey and Ydenberg 2003). The effect of habitat quality on egg survival is likely a rather weak density-dependent mechanism affecting egg survival relative to superimposition. In the case of brook trout observed in Scott Lake, the seasonal timing of spawning by females of different size occurs over a protracted period and may reflect an adaptive response by small females for minimizing density-dependent egg loss by waiting for large females to complete spawning in the limited number of groundwater sites.

The effects of redd superimposition can be particularly acute for small female salmonines. Experimental studies of Pacific salmon show that small (or hatchery) females attempting to breed at the same time as large females incurred greater displacement from territories (van den Berghe and Gross 1989; Foote 1990) or suffered greater delays in the onset of breeding, resulting in a decreased ability to spawn all eggs before death (Fleming and Gross 1993, 1994). Suitable spawning sites appear to be a limiting feature of this brook trout mating system. In Scott Lake, three quarters of

© 2005 NRC Canada

Fig. 6. Distribution of spawning sites used by brook trout (*Salvelinus fontinalis*) in (*a*) 1994 and (*b*) 1995, the corresponding numbers of eggs deposited in (*c*) 1994 and (*d*) 1995, and the estimated numbers of eggs surviving in those sites in relation to groundwater flow scenarios (A, B, and C in Fig. 4*b*) for the (*e*) 1994 and (*f*) 1995 breeding seasons at Scott Lake. Modeled egg survival was least in habitat quality scenario C (solid bars), with additional numbers of eggs surviving under scenarios B (shaded bars) and A (open bars).



all spawning sites were subsequently reused by a different female. The extensive redd superimposition, however, resulted in a realized frequency of redd destruction of about half of this amount (27%–43%) because large females constructed deeper redds and tended to spawn prior to small females. Somewhat higher levels of redd superimposition than observed for this brook trout population have been recorded for other salmonines (e.g., 89%, Hayes 1987; 50%, van den Berghe and Gross 1989; 53%, Essington et al. 1998), as well as low rates of superimposition (4%, Knapp and Vredenburg 1996; 3%–22%, summary in Fleming 1996). In other brook trout populations, high levels of redd superimposition are interpreted as socially facilitated site choice rather than an outcome of spawning site limitation (Essington et al. 1998). Alternatively, others have proposed that redd site choice is a random process (Sorensen et al. 1995). This approach ignores seasonal timing of redd use and crowding effects that can effectively lower the operating density of spawning females on any given day relative to a strict random model of settlement (Blanchfield and Ridgway 1997; Essington et al. 1998).

In Scott Lake, the total number of seepage sites used by spawning brook trout varies among years because peripheral sites with low flow rates increase or decrease in number ap-

© 2005 NRC Canada

parently as a function of rainfall (Ridgway and Blanchfield 1998). Only redd sites with relatively high rates of groundwater flow are used each year (Ridgway and Blanchfield 1998). The effect of redd superimposition on egg survival is therefore likely to vary from year to year depending on the number of redd sites available, the range in flow rates at available sites, and female population size at the time. Female reproductive success in brook trout is not based on a fixed number of redd sites but is an interaction between environmental factors (rainfall and seepage) that affect site availability and competitive interactions among females that vary with year-class size.

Groundwater seepage rate is an essential habitat feature for spawning brook trout in lakes (Fraser 1982; Curry and DeVito 1996; Blanchfield and Ridgway 1997) and an important although not exclusive element for stream-spawning populations (Curry et al. 2002). A single habitat parameter has facilitated our examination of habitat effects on reproductive success as opposed to more commonly used multiparameter models that typically include water depth, substrate characteristics, and flow patterns. The threshold relationship between groundwater seepage rate and embryo survival in Scott Lake is a pattern observed in other relationships linking environmental parameters and egg survival in salmonines (Bjorn and Reiser 1991). At flow rates of 20 $mL \cdot m^{-2} \cdot min^{-1}$ and greater, mean egg survival was relatively constant (37%), while at sites of about half this seepage rate and lower (<11 $mL \cdot m^{-2} \cdot min^{-1}$), there is essentially no survival of eggs. Low flow patterns observed with the use of piezometers in another lake also resulted in a dramatic reduction in egg survival (6%) relative to redds with relatively high flows (~30%–50% survival; Curry et al. 1995). The limited number of spawning sites with high flow rates at Scott Lake produced a bottleneck to the recruitment of young brook trout that substantially lowered female reproductive success.

Groundwater flow was the dominant route through which female brook trout experienced egg loss in our model such that even in the absence of competition for spawning sites, egg survival to emergence was only 9%–33%. The combined influence of female competition and habitat quality resulted in survival of eggs to emergence of approximately 4%–21% in both years of this study. Comparable survival estimates were observed for an egg incubation study at brook trout spawning sites in a lake inlet stream (mean 8.1%; Bernier-Bourgault and Magnan 2002). These estimates of egg to fry survival are similar to those of various Pacific salmon species over the same life history stage (~7% for *O. gorbuscha*, *O. keta*, and *O. nerka* and ~17% for *O. kisutch* at the lower end of survival estimates; Bradford 1995). The wide range in egg to alevin survival for eggs buried in hatchboxes at Scott Lake (0%–59%) is similar to other estimates of survival for the same life history stage of lacustrine brook trout in this region (3%–38% for preferred spawning sites, Fraser 1985; 6%–68%, Curry et al. 1995). The similarity among these studies suggests that the overall low survival of eggs in Scott Lake was not an artefact of using hatchboxes (see Garrett and Bennett 1996) but rather is typical of brook trout under natural conditions.

An empirically stronger route for estimating female reproductive success, compared with the modeling approach adopted in this study, would include redd sampling for egg abundance, genotyping females and offspring, and then determining the scope of redd disruption based on offspring production owing to reuse of sites by females. This approach seems impractical for the Scott Lake population. Many redds were located at 1 m depth and distributed among sand and cobble substrates covered with organic deposits. Furthermore, spawning extended over approximately 60 days in each year (Blanchfield and Ridgway 1997). Sampling substrates for egg abundance would have disrupted spawning habitat and disrupted ongoing mating behaviour over a 2-month period, particularly at sites that received repeated spawning activity. Extensive sampling activity would have compromised a unique feature of the Scott Lake site; specifically the ability to observe in full a salmonine mating system in terms of individually identified breeding adults over the entire spawning season and all available sites. Despite some limitations of the modeling approach, we believe that adopting this route has helped demonstrate the dominant role of habitat quality in the determination of female reproductive success, at least for the period of egg to alevin survival, for a lake-spawning brook trout population.

Reproductive success in this study was examined only in terms of habitat quality and superimposed redds. Predation of newly deposited eggs is known to occur in salmonine mating systems (Maekawa and Ozonato 1986), and it occurs in the mating system of brook trout in Scott Lake as well (Blanchfield and Ridgway 1999). Although estimating the loss of eggs owing to predation/cannibalism is difficult for each spawning event, the magnitude of this factor in overall egg loss can be estimated for the population. Egg cannibalism by peripheral males occurred in 24% of observed spawnings in Scott Lake during the same time period of this study and, on average, two peripheral males were present around each spawning pair of brook trout (range: 0–6 peripheral males; Blanchfield and Ridgway 1999). Maekawa and Ozonato (1986) estimated the loss of eggs to cannibalism in the mating system of Miyabe charr (*Salvelinus malma miyabei*) at ~5–10 eggs consumed per cannibalistic male. Thus, based on the observed frequency of egg cannibalism (24%), and assuming that two males each consume 20 eggs during these events, egg losses owing to cannibalism represent less than 2% of total egg deposition in each breeding season for the Scott Lake population. Loss of eggs to cannibalism is likely small in comparison with losses stemming from redd superimposition and habitat quality.

In summary, groundwater discharge is an important feature of spawning habitat in other *Salvelinus* species (e.g., Cunjak et al. 1986; Baxter and McPhail 1999; Power et al. 1999) along with hyporheic exchange of water (Baxter and Hauer 2000). A significant amount of field work has been invested so far in determining the site characteristics of spawning habitat in brook trout and other members of the char group. For brook trout, this work has demonstrated the importance of groundwater as a feature of spawning sites (Curry et al. 1995; Blanchfield and Ridgway 1997; this study) and its absence as an element of spawning sites in other areas (Fiss and Carline 1993; Curry et al. 2002). Whether spawning sites are indeed fed by groundwater or hyporheic exchange, a real need exists for determining the locations of these features at the landscape level (e.g.,

© 2005 NRC Canada

Baxter and Hauer 2000) where resource planning and conservation efforts for brook trout and other *Salvelinus* species can be more operationally effective.

Acknowledgements

We greatly appreciate the field assistance of Kim Hughes, Kim Mandzy, Lori Flavelle, and Scott Milne during the 1994–1997 fall seasons. We thank Greg Betteridge, Doug Brown, and Gary Ridout for advice and help with the hatchbox experiment and Trevor Middel for interpolation of groundwater seepage data. This paper is part of a thesis submitted by P.J.B. in partial fulfilment of a doctoral degree from the Faculty of Graduate Studies, York University, and has been improved with comments from committee members and other reviewers. Support for this work came from a Dean's Academic Excellence Scholarship, York University (P.J.B.), the Ontario Ministry of Natural Resources, and a Natural Sciences and Engineering Research Council of Canada operating grant (M.S.R.).

References

Baxter, C.V., and Hauer, F.R. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Can. J. Fish. Aquat. Sci. **57**: 1470–1481.

Baxter, J.S., and McPhail, J.D. 1999. The influence of redd site selection, groundwater upwelling, and over-winter incubation temperature on survival of bull trout (*Salvelinus confluentus*) from egg to alevin. Can. J. Zool. **77**: 1233–1239.

Bernier-Bourgault, I., and Magnan, P. 2002. Factors affecting redd site selection, hatching, and emergence of brook charr, *Salvelinus fontinalis*, in an artificially enhanced site. Environ. Biol. Fishes, **64**: 333–341.

Bjorn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. *In* Influences of forest and rangeland management on salmonid fishes and their habitats. *Edited by* W.R. Meehan. Am. Fish. Soc. Spec. Publ. **19**: 83–138.

Blanchfield, P.J., and Ridgway, M.S. 1996. Use of seepage meters to measure groundwater flow at brook trout redds. Trans. Am. Fish. Soc. **125**: 813–818.

Blanchfield, P.J., and Ridgway, M.S. 1997. Reproductive timing and redd site use by lake-spawning brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **54**: 747–756.

Blanchfield, P.J., and Ridgway, M.S. 1999. The cost of peripheral males in a brook trout mating system. Anim. Behav. **57**: 537–544.

Blanchfield, P.J., Ridgway, M.S., and Wilson, C.C. 2003. Breeding success of male brook trout (*Salvelinus fontinalis*) in the wild. Mol. Ecol. **12**: 2417–2428.

Bradford, M.J. 1995. Comparative review of Pacific salmon survival rates. Can. J. Fish. Aquat. Sci. **52**: 1327–1338.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Trans. Am. Fish. Soc. **117**: 1–21.

Crisp, D.T., and Carling, P.A. 1989. Observations on siting, dimensions and structure of salmonid redds. J. Fish Biol. **34**: 119–134.

Cunjak, R.A., Power, G., and Barton, D.R. 1986. Reproductive habitat and behaviour of anadromous arctic char (*Salvelinus alpinus*) in the Koroc River, Quebec. Nat. Can. (Que.), **113**: 383–387.

Curry, R.A., and Devito, K.J. 1996. Hydrogeology of brook trout (*Salvelinus fontinalis*) spawning and incubation habitats: implications for forestry and land use development. Can. J. For. Res. **26**: 767–772.

Curry, R.A., and Noakes, D.L.G. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **52**: 1733–1740.

Curry, R.A., Noakes, D.L.G., and Morgan, G.E. 1995. Groundwater and the incubation and emergence of brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **52**: 1741–1749.

Curry, R.A., Scruton, D.A., and Clarke, K.D. 2002. The thermal regimes of brook trout incubation habitats and evidence of changes during forestry operations. Can. J. For. Res. **32**: 1200–1207.

Embody, G.C. 1934. Relation of temperature to the incubation period of eggs of four species of trout. Trans. Am. Fish. Soc. **64**: 281–289.

Environmental Systems Research Institute. 1992. ArcView GIS version 3.1 [computer program]. ESRI Limited, Redlands, Calif.

Essington, T.E., Sorensen, P.W., and Paron, D.G. 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. Can. J. Fish. Aquat. Sci. **55**: 2310–2316.

Essington, T.E., Quinn, T.P., and Ewert, V.E. 2000. Intra- and interspecific competition and the reproductive success of sympatric Pacific salmon. Can. J. Fish. Aquat. Sci. **57**: 205–213.

Fiss, F.C., and Carline, R.F. 1993. Survival of brook trout embryos in three episodically acidified streams. Trans. Am. Fish. Soc. **122**: 268–278.

Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Rev. Fish Biol. Fish. **6**: 379–416.

Fleming, I.A., and Gross, M.R. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. Ecol. Appl. **3**: 230–245.

Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution, **48**: 637–657.

Foote, C.J. 1990. An experimental comparison of male and female spawning territoriality in a pacific salmon. Behaviour, **115**: 283–314.

Fraser, J.M. 1982. An atypical brook charr (*Salvelinus fontinalis*) spawning area. Environ. Biol. Fishes, **7**: 385–388.

Fraser, J.M. 1985. Shoal spawning of brook trout, *Salvelinus fontinalis*, in a Precambrian shield lake. Nat. Can. (Que.), **112**: 163–174.

Fukushima, M., Quinn, T.P., and Smoker, W.W. 1998. Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. Can. J. Fish. Aquat. Sci. **55**: 618–625.

Garrett, J.W., and Bennett, D.H. 1996. Evaluation of fine sediment intrusion into Whitlock-Vibert boxes. N. Am. J. Fish. Manag. **16**: 448–452.

Geist, D.R. 2000. Hyporheic discharge of river water into fall chinook salmon (*Oncorhynchus tshawytscha*) spawning areas in the Handford Reach, Columbia River. Can. J. Fish. Aquat. Sci. **57**: 1647–1656.

Geist, D.R., Jones, J., Murray, C.J., and Dauble, D.D. 2000. Suitability criteria analyzed at the spatial scale of redd clusters improved estimates of fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat use in the Handford Reach, Columbia River. Can. J. Fish. Aquat. Sci. **57**: 1636–1646.

Godin, J.-G.J. 1982. Migrations of salmonid fishes during early life history phases: daily and annual timing. *In* Proceedings of the Salmon and Trout Migratory Behavior Symposium, 3–5 June

© 2005 NRC Canada

1981, Seattle, Washington. *Edited by* E.L. Brannon and E.O. Salo. University of Washington Press, Seattle, Wash. pp. 22–50.

Hayes, J.W. 1987. Competition for spawning space between brown (*Salmo trutta*) and rainbow trout (*S. gairdneri*) in a lake inlet tributary, New Zealand. Can. J. Fish. Aquat. Sci. **44**: 40–47.

Hendry, A.P., Berg, O.K., and Quinn, T.P. 2001. Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). Oikos, **93**: 407–418.

Holtby, L.B., and Healey, M.C. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **43**: 1946–1959.

Houpes, D.T. 1972. Selection of spawning sites by sockeye salmon in small streams. Fish. Bull. **70**: 447–458.

Knapp, R.A., and Preisler, H.K. 1999. Is it possible to predict habitat use of spawning salmonids? A test using California golden trout (*Oncorhynchus mykiss aguabonita*). Can. J. Fish. Aquat. Sci. **56**: 1576–1584.

Knapp, R.A., and Vredenburg, V.T. 1996. Spawning by California golden trout: characteristics of spawning fish, seasonal and daily timing, redd characteristics, and microhabitat preferences. Trans. Am. Fish. Soc. **125**: 519–531.

Knapp, R.A., Vredenburg, V.T., and Matthews, K.R. 1998. Effects of stream channel morphology on golden trout spawning habitat and recruitment. Ecol. Appl. **8**: 1104–1117.

Latta, W.C. 1965. Relationship of young-of-the-year trout to mature trout and groundwater. Trans. Am. Fish. Soc. **94**: 32–39.

Maekawa, K., and Hino, T. 1990. Spawning tactics of female Miyabe charr (*Salvelinus malma miyabei*) against egg cannibalism. Can. J. Zool. **68**: 889–894.

Maekawa, K., and Ozonato, N. 1986. Reproductive tactics and fertilization success of mature male Miyabe charr, *Salvelinus malma miyabei*. Environ. Biol. Fishes, **15**: 119–129.

McNeil, W.J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. J. Fish. Res. Board Can. **21**: 1385–1396.

McNeil, W.J. 1966. Distribution of spawning pink salmon in Sashin Creek, southeastern Alaska, and survival of their progeny. U.S. Fish Wildl. Serv. Sci. Rep. 538.

McPhee, M.V., and Quinn, T.P. 1998. Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka*. Environ. Biol. Fishes, **51**: 369–375.

Morbey, Y.E., and Ydenberg, R.C. 2003. Timing games in the reproductive phenology of female Pacific salmon (*Oncorhynchus* spp.). Am. Nat. **161**: 284–298.

Power, G., Brown, R.S., and Imhof, J.G. 1999. Groundwater and fish — insights from northern North America. Hydrol. Processes, **13**: 401–422.

Quinn, N.W.S., Korver, R.M., Hicks, F.J., Monroe, B.P., and Hawkins, R.R. 1994. An empirical model of lentic brook trout. N. Am. J. Fish. Manag. **14**: 692–709.

Reiser, D.W., and Wesche, T.A. 1977. Determination of physical and hydraulic preferences of brown and brook trout in the selection of spawning locations. Comp. Rep. Water Res. Ser. No. 64.

Ridgway, M.S., and Blanchfield, P.J. 1998. Brook trout spawning areas in lakes. Ecol. Freshw. Fish, **7**:140–145.

Sorensen, P.W., Cardwell, J.R., Essington, T., and Weigel, D.E. 1995. Reproductive interactions between sympatric brook and brown trout in a small Minnesota stream. Can. J. Fish. Aquat. Sci. **52**: 1958–1965.

Sowden, T.K., and Power, G. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. Trans. Am. Fish. Soc. **114**: 804–812.

Steen, R.P., and Quinn, T.P. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. Can. J. Zool. **77**: 836–841.

van den Berghe, E.P., and Gross, M.R. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution, **43**: 125–140.

Vladykov, V.D. 1956. Fecundity of wild speckled trout (*Salvelinus fontinalis*) in Quebec lakes. J. Fish. Res. Board Can. **13**: 799–841.

© 2005 NRC Canada

The relationship between piscivory and growth of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*) in headwater lakes of the Canadian Shield

Andrea Bertolo and Pierre Magnan

Abstract: We used data from a survey of 36 headwater lakes of the Canadian Shield to investigate the relationship between piscivory and growth, abundance, and longevity of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*). The occurrence of northern pike (*Esox lucius*) and walleye (*Sander vitreus*) explained variations in the abundance of both white sucker and yellow perch, suggesting strong predation-induced mortality. The longevity of both species tended to be negatively related to increased piscivory. White sucker grew better and had a better condition in lakes with piscivores. Yellow perch showed only small among-lake differences in growth and condition. The superior competitive ability of white sucker over yellow perch could explain why yellow perch did not show improved growth or longevity where population densities were low in lakes with piscivores and white sucker. Furthermore, yellow perch growth was inversely related to the biomass of piscivorous fish in their first year of life. Stomach content data suggest that small yellow perch, which rely on zooplankton, might restrict their use of pelagic resources to reduce their predation risk by piscivores, thus reducing their growth. Our results show that the effects of piscivores can be species-specific and dependent on community structure.

Résumé : Nous avons utilisé les données d'un inventaire de 36 lacs du bouclier canadien pour examiner la relation entre la piscivorie et la croissance, l'abondance ainsi que la longévité du meunier noir (*Catostomus commersoni*) et de la perchaude (*Perca flavescens*). L'occurrence du grand brochet (*Esox lucius*) et du doré jaune (*Sander vitreus*) ont expliqué les variations d'abondance du meunier noir et de la perchaude, suggérant une forte mortalité due à la prédation. La longévité des deux espèces tendait à diminuer en fonction du gradient de piscivorie. Le meunier noir a affiché une meilleure croissance et une meilleure condition dans les lacs avec piscivores. La perchaude n'a montré que des faibles différences de croissance entre les lacs étudiés. La supériorité compétitive du meunier noir sur la perchaude pourrait expliquer pourquoi la perchaude n'a pas profité de la réduction de sa densité dans les lacs avec piscivores et meuniers noirs. De plus, la croissance de la perchaude était inversement reliée à la biomasse des piscivores dans leur première année de vie. L'analyse des contenus stomacaux suggère que les perchaudes juvéniles, qui dépendent du zooplancton, pourraient réduire leur utilisation des ressources pélagiques pour diminuer leur risque de prédation par les piscivores, réduisant ainsi leur croissance. Nos résultats illustrent que les effets de la piscivorie peuvent être spécifiques à l'espèce et dépendants de la structure de la communauté.

Introduction

Piscivory is known to exert strong effects on abundance, biomass, and diversity of prey fish (Carpenter and Kitchell 1993; Chapleau et al. 1997). Food web theory suggests that such a top-down control can potentially lead to major changes in the biomass of lower trophic levels in lake ecosystems (Carpenter and Kitchell 1993). For example, by lowering the levels of intraspecific competition, the reduction of prey fish density by piscivores might lead to better growth in surviving individuals. In contrast, the dynamics of competitive interaction among prey species could be such that some species would not experience any growth improvement in response to a decrease in intraspecific competition related to piscivory (e.g., low competitive ability compared with other prey fish species). It is thus important to understand how different prey species respond to piscivory to better understand the effects of changes at the top of lacustrine food webs.

It is well documented that the growth of widely distributed species such as white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*) can differ among popu-

Received 16 August 2004. Accepted 24 May 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 26 October 2005.
J18268

A. Bertolo[1] and P. Magnan. Groupe de recherche sur les écosystèmes aquatiques, Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, QC G9A 5H7, Canada.

[1]Corresponding author (e-mail: andrea_bertolo@uqtr.ca).

 doi: 10.1139/F05-174 © 2005 NRC Canada

Table 1. Selected watershed characteristics and morphometric variables of the study lakes.

Variable	Lake group			F	P
	I (n = 10)	II (n = 17)	III (n = 9)		
Lake area (km^2)	0.67±0.61	0.36±0.17	0.46±0.20	2.65	0.09
Maximum depth (m)	14.8±7.4	14.3±6.1	11.9±4.7	0.83	0.44
Mean depth (m)	5.3±2.2	4.6±1.8	4.7±1.7	0.43	0.65
Watershed area (km^2)	3.6±3.6	3.0±1.9	4.9±6.4	0.65	0.53
Residence time (years)	2.2±1.4	1.4±0.8	1.4±1.1	2.35	0.11
Lake slope (%)	7.0±3.2	8.9±4.0	6.2±2.0	1.84	0.17

Note: Data are means ± SD. Lake groups: I, no piscivores; II, with northern pike (*Esox lucius*); III, with northern pike and walleye (*Sander vitreus*). F and P values as determined by ANOVA conducted on log-transformed data are also shown.

lations (Trippel and Harvey 1987; Boisclair and Leggett 1989*a*; Chen and Harvey 1999). However, factors explaining such variations are still unclear. Different pathways, related to a combination of density-dependent (i.e., biotic) and density-independent (i.e., abiotic) factors, could lead to among-lake variability in fish growth. A strong variation in the length-at-age of 32 white sucker populations was observed by Chen and Harvey (1999), who related these among-lake differences to spatial (genetic difference owing to isolation) and physicochemical (lake pH) factors. Many studies have been conducted on *Perca* spp., and several nonmutually exclusive interpretations have been suggested to explain variations in their growth, including prey type (Tyson and Knight 2001), habitat productivity (Abbey and Mackay 1991), water temperature (Power and van den Heuvel 1999), and the presence of competing species (Hayes et al. 1992). Boisclair and Leggett (1989*a*, 1989*b*) found that neither the quantity nor the mean size of the ingested prey was able to fully explain the strong among-population variations in yellow perch growth rates. They suggested that the low growth of yellow perch was related to an increase in their metabolic demand caused by frequent interactions with cyprinid fish (Boisclair and Leggett 1989*c*). This example suggests that community structure could affect fish growth patterns by modifying the behaviour of individuals. The presence of piscivorous fish could also have strong effects on prey fish behaviour and consequently on their growth because they are forced to use suboptimal foraging habitats (Werner et al. 1983). In contrast, as mentioned above, predation can have an indirect positive effect on fish growth by reducing the level of intra- and inter-specific competition (Rudstam et al. 1996; Paukert et al. 2002).

Because yellow perch and white sucker show ontogenetic differences in habitat use and body size, they are potentially exposed to different predation risks during their whole life. Yellow perch is a generalist feeder that shows ontogenetic shifts in both diet and habitat: after hatching in the littoral zone, the individuals migrate to the pelagic zone to feed on zooplankton and then return to the littoral zone when they have a sufficient gape size to integrate benthic prey into their diet (Post et al. 1997). In contrast, white sucker has a short planktivorous stage and relies on benthic resources during most of its ontogeny (Scott and Crossman 1973). Because of its pelagic phase and the use of zooplankton as an alternative resource in the presence of competitors, yellow perch is probably more exposed than white sucker to piscivorous predators that occur at the interface of the pelagic and littoral zones. Given that the duration of the planktonic stage is important in determining the growth pattern of 0+ yellow perch (Post et al. 1997), piscivorous predators might affect the growth of 0+ yellow perch by forcing them to an earlier habitat shift, thus reducing their feeding on zooplankton. Furthermore, because white sucker can reach larger sizes than yellow perch, it is probably less vulnerable to gape-limited predators than yellow perch. Because the interplay of behavioural and numeric effects of piscivorous fish is likely to be habitat and species dependent, white sucker and yellow perch might respond differently to the presence of piscivores.

In this paper, we test the hypothesis that predation by piscivorous fish is related to variations in the growth of white sucker and yellow perch using data from a survey of 36 Canadian Shield lakes that contain at least one of these two species. We expected predation by piscivorous fish to be associated with (*i*) a higher growth and (or) condition of both prey species because of their relatively low abundance and (*ii*) a poor growth and (or) condition of those size classes of yellow perch that rely on zooplankton, owing to a presumably restricted access to the pelagic resources. The study lakes are in the same geographic region and have similar morphometry, so they are comparable in many respects. In contrast, the biomass of large piscivorous predators differs greatly among the study lakes, thus allowing the analysis of their effect on the growth of both white sucker and yellow perch. Lake morphometric variables were included in the analysis to control for their potential indirect effects on fish growth.

Methods

Study area and biological background

Thirty-six thermally stratified headwater lakes were selected on the basis of comparable size, basin morphometry, and catchment properties (Table 1). The lakes were accessible only by aircraft, belong to the same hydrographic region, and are located in a 30 000 km^2 area surrounding the Gouin Reservoir, Haute-Mauricie, Quebec, Canada (48°50′N, 75°00′W) (see fig. 1 in Carignan et al. 2000). Lake morphometry and catchment properties were determined from aerial photographs and from 15–25 echosounder transects (Carignan et al. 2000). The catchments of these lakes were only exposed to limited perturbation until 1995, when nine of them experienced forest fires and nine were logged by forestry companies. The effects of forest fires and logging

© 2005 NRC Canada

Table 2. Relative biomass (BPUE) (*g* fresh weight·net^{-1}·night^{-1}) and numbers (CPUE) (individuals·net^{-1}·night^{-1}) of major fish taxa in the study lakes.

Variable		Lake group				
		I (n = 10)	II (n = 17)	III (n = 9)	F	P
Brook trout	BPUE	694±519 (6)	0±0 (0)	0±0 (0)	nt	
	CPUE	5.6±6.4	0±0	0±0	nt	
Yellow perch	BPUE[a]	704±674 (3)	177±135 (13)	144±174 (9)	3.1	0.068
	CPUE[a]	64.5±59.5a	11.8±7.3b	8.1±5.9b	7.4	0.0034*
White sucker	BPUE[b]	3476±1812 (10)	1715±2519 (13)	2201±2227 (8)	3.1	0.059
	CPUE[a]	18.9±12.0a	2.9±3.4b	3.9±3.1b	12.7	0.0001*
Northern pike	BPUE	0±0 (0)	2696±1384 (17)	2228±1154 (9)	nt	
	CPUE	0±0	2.5±1.4	1.5±0.7	nt	
Walleye	BPUE	0±0 (0)	0±0 (0)	3573±1609 (9)	nt	
	CPUE	0±0	0±0	8.1±3.6	nt	
Lake whitefish	BPUE	0±0 (0)	1454±908 (3)	3243±2584 (8)	nt	
	CPUE	0±0	6.1±7.4	8.0±7.0	nt	
Prey fish	BPUE[c]	255±204a (9)	104±189ab (12)	36±60b (6)	4.9	0.016
	CPUE[c]	45.8±49.5a	18.3±23.9ab	6.3±9.8b	5.71	0.009*

Note: Data are means ± SD. Means with different letters are significantly different as determined by a Tukey multiple range comparison test (P < 0.05). Prey fish are all small-bodied species (mainly cyprinids) pooled. The occurrence of each fish species is indicated in parentheses. nt, not tested owing to low sample size. An asterisk denotes significant after the sequential Bonferroni correction. Lake groups: I, no piscivores; II, with northern pike (*Esox lucius*); III, with northern pike and walleye (*Sander vitreus*).

[a]ANOVA performed on data that were log transformed.

[b]ANOVA performed on data that were square-root transformed.

[c]ANOVA performed on data that were rank transformed.

were studied on these lakes for the 3 years following the perturbation (between 1996 and 1998). Carignan et al. (2000) showed that fire and logging were associated with higher concentrations of nutrients and major ions in these lakes. Planas et al. (2000) found significant effects of the perturbations on the biomass of both benthic and pelagic algae, which were higher in logged and burned lakes between 1996 and 1998. Furthermore, Patoine et al. (2000) found that the biomass of small-sized zooplankton (mostly rotifers) was higher in burned-watershed lakes, while the biomass of larger zooplankton (mostly calanoids) was lower in logged-watershed lakes. Between 1996 and 1997, St-Onge and Magnan (2000) found some negative effects of these perturbations on the abundance of small size classes of both yellow perch and white sucker but did not observe such an effect for larger individuals. In addition, watershed perturbations had no effect on the growth of yellow perch in these lakes (St-Onge and Magnan 2000; growth of white sucker was not estimated in this study). Despite the lack of any clear effects on yellow perch growth, we cannot exclude the possibility that such perturbations could affect the entire structure of the food web over the long term and indirectly affect fish growth. Since we focus here on the effects of fish community structure, we adopted two different approaches to control for the effects of perturbations on fish growth. First, to avoid the potential noise in fish growth owing to the watershed perturbation, we used only back-calculated lengths-at-age of fish from the period preceding the watershed perturbations in our analysis. Second, variables describing the degree of perturbation in the watershed (see below) were included in the list of independent variables used to explain variation in the length–weight relationships.

Twenty-three fish species were found in this survey. Northern pike (*Esox lucius*), white sucker, lake whitefish (*Coregonus clupeaformis*), walleye (*Sander vitreus*, formerly *Stizostedion vitreum*), yellow perch, and brook trout (*Salvelinus fontinalis*) were the most important in terms of relative biomass (for a complete list, see St-Onge and Magnan 2000). For this analysis, the numbers and relative biomasses of other small prey fish (mostly cyprinids) were pooled into a single prey category (Table 2). The relative biomasses (grams of fish per gill net per night; see below) of these seven taxa were used as explanatory variables in subsequent analyses to explain variations in white sucker and yellow perch growth.

For the purpose of the present study, we classified the fish communities into three categories: group I, absence of large piscivorous predators; group II, presence of northern pike; and group III, co-occurrence of northern pike and walleye. Fish community and watershed perturbation were not confounding factors in this study, since a similar proportion of the lakes with each type of fish community experienced watershed perturbations.

Fish sampling

Nineteen lakes were sampled in 1996 and 17 in 1997. Each lake was sampled once between June and August. The sampling date (as Julian days) was not significantly different among lake groups (one-way analysis of variance (ANOVA), $F_{(2,35)} = 1.1$, $P = 0.36$). Fish were captured with experimental monofilament gill nets that were 102.3 m long × 2.7 m high with stretched mesh panels of 20, 24, 33, 36, 50, 60, 76, 90, and 100 mm (filament diameter of 0.17, 0.20, 0.20, 0.20, 0.20, 0.32, 0.32, 0.32, and 0.32 mm, respectively). Gill nets were set perpendicular to the shore, with small and large meshes alternating from the shore among gill nets. The nets were set at regular intervals around the lake, with the first net location being randomly located on aerial photo-

© 2005 NRC Canada

graphs. The fishing effort was six nets per night for lakes <50 ha, eight nets per night for lakes of 50–100 ha, 10 nets per night for lakes of 100–150 ha, and 12 nets per night for lakes >150 ha. The nets fished for 17–19 h, covering the period between 1600 and 1030. For all fish captured, total length (±1 mm) and weight (±0.1 g) were noted. This procedure led to comparable among-lake estimates of catch and biomass per unit effort (CPUE and BPUE, respectively, numbers and grams of fish captured per net per night). To determine age and growth, we used fin rays for white sucker and opercular bones for yellow perch. Details on age determination can be found in St-Onge and Magnan (2000) for yellow perch and in Brodeur et al. (2001) for white sucker. Longevity was measured as the 90th percentile of the fish ages observed in a given lake.

Stomach content analysis

To get indirect information on habitat use, we analyzed the stomach contents of both yellow perch and white sucker. The diet of a subsample of these two species was determined to compare their feeding habits among lake groups. The stomach content was analyzed for yellow perch, while the anterior two thirds of the gut was analyzed for white sucker, since this species lacks a true stomach (Tremblay and Magnan 1991). Prey items were classified into four functional groups as zoobenthos, zooplankton (microcrustaceans and *Chaoborus* larvae), dipteran pupae, and prey fish. Each prey category was dried (12 h at 60 °C) and then weighed to the nearest 0.0001 g. Because of the reduced sample size, it was not possible to analyze gut contents for many size classes. However, to investigate the potential ontogenetic shifts occurring in white sucker and yellow perch among lake groups, we pooled the data into two arbitrary size classes (i.e., small and large fish), corresponding to fish <200 and ≥200 mm for white sucker and <90 and ≥90 mm for yellow perch. Statistical analyses were carried out only for those lakes where we had at least three gut contents per size class, although the sample size was >10 in most of the lakes. We analyzed (mean ± SD) 29.5 ± 26.0 and 32.6 ± 26.9 stomachs per lake for white sucker <200 and ≥200 mm, respectively, and 25.3 ± 24.7 and 37.9 ± 35.8 stomachs per lake for yellow perch <90 and ≥90 mm, respectively. Since logging and fire occurred before the fish were collected, these watershed perturbations might have affected the fish diet. However, since watershed perturbation was not different among the lake groups (i.e., fish community types), it could only have added noise in the analysis of this last factor but not biased the results.

Statistical analyses

Relative abundance, longevity, and diet

We analyzed the variations among lake groups in the relative abundance (CPUE and BPUE) of the seven fish taxa studied as well as in the longevity of yellow perch and white sucker with one-way ANOVA followed by Tukey multiple range comparison tests. A two-way ANOVA was used to test the effects of fish size and lake group on the feeding habits. When necessary, data were $\log(x + 1)$ or square root transformed to normalize the residuals. Percentage data (i.e., the proportion of different prey types in the stomachs) were arcsine transformed prior to analysis. If these procedures were not successful, ANOVAs were conducted on rank-transformed data (Quinn and Keough 2002).

Growth

We used two approaches to investigate the determinants of fish growth in our study lakes: (*i*) comparison of growth trajectories among lake groups with linear mixed models to determine the effect of piscivores on fish growth and (*ii*) multiple linear regression to determine if length-at-age of the main age classes is affected by factors other than piscivores (e.g., lake morphometry).

Linear mixed models (procedure MIXED, SAS statistical package; SAS 1999) were used to compare fish growth trajectories among lake groups because this statistical approach properly handles both fixed (e.g., lake groups) and random (e.g., lakes) factors. Furthermore, linear mixed modeling is appropriate for use with repeated measures, like back-calculated lengths from the same fish, that are not independent (Littell et al. 1996). Within this framework, both the autocorrelation among back-calculated lengths and their covariance can be modeled by selecting an appropriate covariance structure (see below) for the matrix of repeated measures (Littell et al. 1996). This is particularly important not only to obtain correct estimates of the regression coefficients but also because the use of an inappropriate covariance structure may lead to invalid significance tests (Littell et al. 1996).

We modeled the data by using a third-order polynomial growth function:

$$\begin{aligned}\mathrm{TL} = {} & a + b \times \mathrm{AGE} + c \times \mathrm{GROUP} \\ & + d \times \mathrm{LAKE(GROUP)} + e \times \mathrm{AGE} \times \mathrm{GROUP} \\ & + f \times \mathrm{AGE}^2 + g \times \mathrm{AGE}^2 \times \mathrm{GROUP} \\ & + h \times \mathrm{AGE}^3 + i \times \mathrm{AGE}^3 \times \mathrm{GROUP}\end{aligned}$$

where TL is fish total length, AGE is fish age (a fixed factor with repeated measures), GROUP is the lake group (a fixed factor), LAKE is the lake from which the fish were caught (a random factor nested into the GROUP factor), and a to i are the regression coefficients. Since yellow perch data were only available for ages 1 and 2, second- and third-order terms were not included and their growth was thus modeled as linear.

The proper covariance structure was chosen by comparing the fit of the model with four different covariance structures (Littell et al. 1996; Verbeke and Molenberghs 2000): (*i*) autoregressive of order one (AR1), (*ii*) compound symmetry (CS), (*iii*) Huynh–Feldt (HF), and (*iv*) unstructured (UN). The AR1 covariance structure assumes that the repeated measures have the same variance, whereas their correlation decreases with increasing lag between them. The CS covariance structure assumes the same variance for all of the repeated measures and that all pairs of repeated measures on the same fish have the same correlation. The HF covariance structure is a generalization of the CS structure, with heterogeneous variance among the repeated measures. Finally, the more general UN covariance structure makes no assumption on the homogeneity of variances or about correlations between repeated measures. The number of parameters needed

© 2005 NRC Canada

to estimate these four covariance structures varies: two for AR1 and CS, $1 + n$ for HF, where n is the number of repeated measures, and $n(n + 1) \times 0.5$ for UN (Littell et al. 1996). An objective comparison of different covariance structures can be done by using goodness-of-fit criteria such as the Akaike information criterion (Littell et al. 1996; Verbeke and Molenberghs 2000). The Akaike information criterion takes into account both the fit of the data and the number of parameters involved in the construction of the covariance matrix, favouring those models with a small number of parameters in the covariance structure (Littell et al. 1996). The selection of the best-fitted and more parsimonious model was carried out by choosing the model with the smaller Akaike information criterion value.

After having selected an appropriate covariance structure, we checked if the order of the polynomial could be reduced (Verbeke and Molenberghs 2000). Thus, if higher-order terms (i.e., AGE^3 and $AGE^3 \times GROUP$) were not significantly related to fish length, they were dropped from the model. The procedure was then applied to higher-order terms (i.e., AGE^2 and $AGE^2 \times GROUP$) in the reduced model. This hierarchical procedure was used to reduce the model until a significant term was found, whether lower-order terms were significant or not (Verbeke and Molenberghs 2000).

If a model with an order lower than three was selected, we used the residual plot to compare the fit of the untransformed model with the fit of an equivalent model in which both the independent and the dependent variables were log transformed. Chen et al. (1992) suggested that such a transformation could greatly improve the fit of a second-order polynomial to model fish growth.

Back-calculated data related to the year of perturbation and the postperturbation period were excluded from the analysis. A minimum of four back-calculated lengths per white sucker and two per yellow perch were used. Moreover, we included in the model only those lakes for which the sample size per age class was three or more individual fish and we restricted the analysis to those ages for which we had at least two lakes per group and per age class. Therefore, back-calculated growth trajectories of white sucker and yellow perch were truncated at age 6 and age 2, respectively. A total of 590 white sucker and 303 yellow perch from 17 and 19 lakes, respectively, were used in this analysis. Globally, a total of 3528 and 606 measures of length-at-age were used in the analysis for white sucker and yellow perch, respectively. If a significant GROUP or GROUP × AGE^n effect was detected, we compared the growth trajectories among lake groups. This was done by pairwise comparisons of adjusted lengths (i.e., least square means of lengths) at different ages. A sequential Bonferroni correction was applied to control for multiple comparisons.

We used stepwise multiple regression to test the hypothesis that differences in lengths-at-age for both white sucker and yellow perch were related to differences in the structure of the fish community (BPUEs of piscivorous fish and of other fish taxa) and in lake morphometry (i.e., altitude, lake area, shoreline development, maximum depth, average lake slope, residence time, basin area, and drainage area to lake area ratio).

Fish condition

The effect of fish community structure on fish condition was analyzed through length–weight relationships. To analyze the effect of lake group on the length–weight relationship for both white sucker and yellow perch, we investigated whether the variation in the fish body weight (W) was related to three main variables and two interactions terms in a linear mixed model:

$$\log W = a + b \times \log \text{TL} + c \times \text{GROUP} + d \times \text{LAKE(GROUP)} + e \times \text{GROUP} \times \log \text{TL} + f \times \text{LAKE(GROUP)} \times \log \text{TL}$$

Julian day and the percentages of watershed burned or logged were used as covariables in this analysis but were discarded if not significantly related to the dependent variable. Pairwise comparisons of adjusted weights (i.e., least square means of log W) allowed us to compare the condition of fish among lake groups. When the slopes among lake groups were significantly different, we compared the adjusted weights for three different sizes representing the range encountered in the populations (i.e., the 25th, 50th, and 75th percentiles of log TL; Littell et al. 1996). Significantly different slopes among lake groups indicate that the differences in fish condition among lake groups vary with fish size, making it necessary to compare their elevation at different values (percentiles) of the independent variable. In the model, we included only the lakes for which the total number of fish measured per lake was ≥10. Comparisons of the length–weight relationships were made for a range of body lengths corresponding to a complete overlap among lake groups. Thus, based on the visual inspection of raw data, we restricted the analysis to white sucker ranging between 100 and 400 mm and to yellow perch <140 mm. A total of 1270 white sucker and 2006 yellow perch from 17 and 24 lakes, respectively, were used in the analysis.

Residual scatterplots, normal probability plots, and partial residual plots were used to determine if the assumptions of models were satisfied (i.e., normality, linearity, and homoscedasticity of residuals). These assumptions were met for all models presented in this paper.

Results

Relative abundance (CPUE and BPUE)

In the absence of both northern pike and walleye (group I), the CPUEs of both white sucker and yellow perch were significantly higher than in lake groups II and III (Table 2). The variations in BPUEs among lake groups of both white sucker and yellow perch tended to be similar to the variations observed in CPUEs, although only marginally significant (Table 2).

Growth

Mixed models

It was not possible to model the white sucker growth data by a third-order polynomial function, since the maximum likelihood estimation technique procedure failed to converge. Therefore, we dropped all of the third-order terms from the model. White sucker growth was best modeled by a

© 2005 NRC Canada

log-transformed second-order polynomial model with a UN covariance structure. The lake group effect was significant ($P = 0.044$), as were both the first- and the second-order interactions between lake group and age (log AGE × GROUP and log AGE^2 × GROUP) (Table 3). Also, both the first- and second-order terms of log AGE were significant (Table 3). This suggests that the observed growth pattern for this species (*i*) is not linear (the log AGE^2 term is significant) and (*ii*) differs among the lake groups (the log AGE^2 × GROUP and log AGE × GROUP terms are significant). In all cases, length-at-age tended to be relatively high in group III, low in group I, and intermediate in group II (Fig. 1). However, pairwise comparisons of adjusted lengths did not show any significant differences between pairs of lake groups.

Yellow perch growth was best modeled by a log-transformed model with a UN covariance structure. Yellow perch showed no significant differences among lake groups, but we found a significant interaction between log AGE and GROUP (Table 3). Age was also significantly related to length (Table 3). Post hoc comparisons of adjusted lengths did not show any significant difference among lake groups.

Table 3. Results of linear mixed models explaining the variation in length of (*a*) white sucker (*Catostomus commersoni*) (1–6 years old, 17 lakes) and (*b*) yellow perch (*Perca flavescens*) (1–2 years old, 19 lakes).

	Type 3 test of fixed effects		
Effect	*df*	*F*	*P*
White sucker			
log AGE	1,575	190.7	<0.0001
GROUP	2,13.9	3.93	0.044
log AGE × GROUP	2,581	29.7	<0.0001
log AGE^2	1,501	648.2	<0.0001
log AGE^2 × GROUP	2,514	12.9	<0.0001
Yellow perch			
log AGE	1,300	4111.2	<0.0001
GROUP	2,15.9	2.38	0.13
log AGE × GROUP	2,300	6.16	0.0024

Note: AGE, fish age (years); GROUP, lake group (see Table 1). log AGE^2 and log AGE^2 × GROUP represent terms for a second-order polynomial model with interactions. A total of 590 and 303 individual growth trajectories were used in this analysis for white sucker and yellow perch, respectively.

Stepwise regressions

The stepwise regression approach revealed that the biomass of piscivorous fish had a strong positive effect on the length of white sucker from age 1 to 6 (Table 4). The length of white sucker at age 1 was directly related to the BPUE of piscivorous fish and white sucker and indirectly related to that of yellow perch (Table 4). The significance level of this latter independent variable (i.e., yellow perch BPUE) proved to be very sensitive to one outlier and was unrelated to the length of white sucker at age 1 after this outlier was omitted from the analysis. In contrast, the BPUEs of piscivorous fish and white sucker were not sensitive to outliers and together explained nearly 55% of the variation in white sucker length-at-age (Table 4). A similar picture was observed for white sucker length-at-age 3, with the BPUE of piscivorous fish, white sucker, and lake whitefish being retained in the regression model (Table 4). For length-at-ages 2, 4, 5, and 6, only the BPUE of piscivorous fish was retained in the models (Table 4). In all models, piscivorous fish biomass was directly related to white sucker length-at-age and explained the largest proportion of the explained variation (Table 4). All stepwise regressions were significant after the sequential Bonferroni correction.

The yellow perch length-at-age 1 was negatively related to the BPUE of piscivorous fish (Table 4). Yellow perch length-at-age 2 was directly related to the total BPUE of yellow perch. Both models were significant after the sequential Bonferroni correction. No lake morphometric variables were selected in any of the models built for the two species.

Length–weight relationships

We found a significant lake group effect in the length–weight relationships for both white sucker and yellow perch (Table 5). Furthermore, there was a significant interaction between the $\log_{10}$ TL and the lake group in both cases, indicating that the slope of the length–weight relationship differed among lake groups. The among-lake pairwise comparisons of white sucker adjusted weights at 180, 205, and 286 mm (the 25th, 50th, and 75th percentiles of log TL, respectively) revealed that in all cases, group I differed significantly from groups II and III, while the latter two were not significantly different (Table 5). For yellow perch, none of the adjusted weights were significantly different among lake groups, but adjusted weights tended to be lower in lake group I, intermediate in group II, and highest in group III (Table 5). The significance of these hypotheses was assessed after a sequential Bonferroni corrected level because a total of nine post hoc comparisons were made for each species. Julian day and the percentages of watershed burned or logged were not significantly related to the dependent variable and therefore were not included in the model.

Longevity

White sucker longevity showed no significant differences among lake groups (one-way ANOVA, $P = 0.27$) but tended to be higher in group I (10.7 ± 2.1 years (mean ± 1 SD), $n = 9$), intermediate in the group II (9.6 ± 2.7 years, $n = 5$), and lower in group III (7.7 ± 4.4 years, $n = 4$). Yellow perch also showed no significant differences in longevity among lake groups (one-way ANOVA, $P = 0.19$; group I, 4.0 ± 2.6 years, $n = 3$; group II, 3.8 ± 1.1 years, $n = 13$; group III, 2.9 ± 0.6 years, $n = 9$).

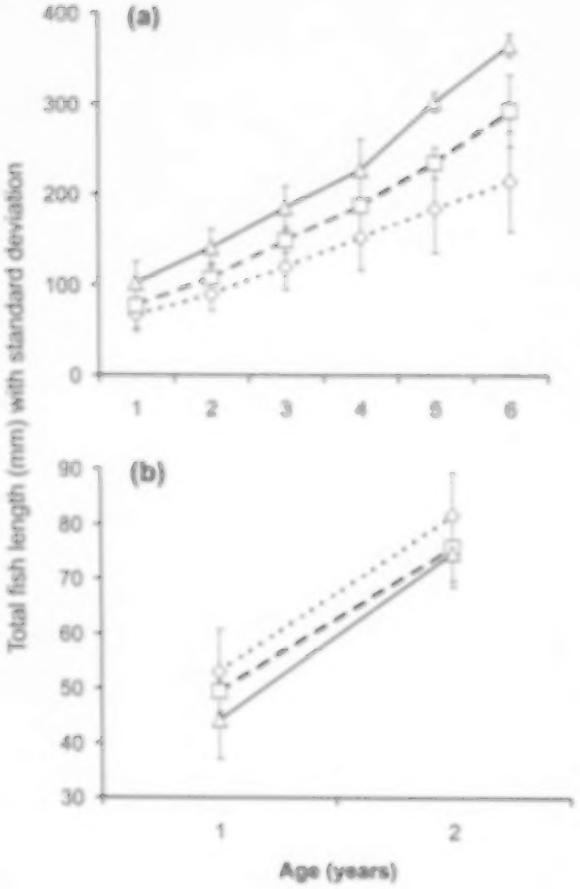
Feeding habits

Zoobenthic organisms were the main prey item in the diet of both size classes of white sucker and represented at least 85% of the gut content dry weight in all cases (Fig. 2). The fraction of zoobenthic organisms varied only among size classes (two-way ANOVA: model, $P = 0.0035$; size class, $P = 0.0004$; group, $P = 0.80$; $n = 22$), while the fraction of other prey items did not vary significantly either between size classes or among lake groups (Fig. 2).

The proportion of zooplankton in the diet of yellow perch was significantly related to both body size and lake group, decreasing from lake group I to lake groups II and III and

© 2005 NRC Canada

Fig. 1. (*a*) White sucker (*Catostomus commersoni*) and (*b*) yellow perch (*Perca flavescens*) growth trajectories. Lake groups: I, no piscivores (diamonds); II, with northern pike (*Esox lucius*) (squares); III, with northern pike and walleye (*Sander vitreus*) (triangles).



from small to large individuals (two-way ANOVA: model, $P = 0.0003$; size class, $P = 0.0004$; group, $P = 0.0078$; $n = 32$) (Fig. 2). The proportion of dipteran pupae decreased significantly with fish size but not among lake groups (two-way ANOVA: model, $P = 0.033$; size class, $P = 0.015$; group, $P = 0.19$; $n = 32$). The fraction of zoobenthos and prey fish did not show any significant difference among lake groups.

Discussion

This study shows that the abundance of piscivorous fish can have species-specific effects on the growth of white sucker and yellow perch. The growth of white sucker was higher in the presence of piscivorous fish, while that of yellow perch was not significantly different among lake groups and tended to be lower in the presence of piscivorous fish.

The relative abundance (CPUE) of white sucker was lower in the presence than in the absence of piscivorous fish. This result, coupled with the positive association between piscivory and both the growth and condition of white sucker, suggests that predation might have increased the mortality of white sucker, which in turn increased its growth by a release of intraspecific competition. The better growth and condition of white sucker from lake groups II and III compared with lake group I supports the hypothesis of an increased per capita availability of benthic resources with the increase of piscivory. The positive correlation between white sucker length-at-age 1–6 and the biomass of piscivorous fish gives complementary support to this interpretation.

Despite the apparent reduction in the levels of intra- and inter-specific competition by white sucker in lakes with northern pike and walleye, yellow perch growth was only slightly affected by piscivorous fish. Moreover, while white sucker growth and condition showed a positive response to piscivorous predation, only yellow perch condition showed a similar response. Yellow perch growth was negatively, although slightly, affected by the presence of piscivores during its first year. The superior competitive ability of white sucker over yellow perch could explain why yellow perch did not profit from its relatively low population density in lakes with piscivores and white sucker. Furthermore, yellow perch growth was inversely related to the biomass of piscivores in their first year of life. Stomach content data suggest that small yellow perch, which rely on zooplankton, might restrict their use of pelagic resources to reduce their predation risk by piscivores, thus reducing their growth. The lack of a significant relationship between piscivorous fish biomass and the length of age-2 yellow perch also suggests that the effects of piscivores were age specific, in contrast with what was observed for white sucker. Our results are in agreement with those of Olson et al. (2001), who suggested that stocking lakes with walleye could negatively affect the growth of small yellow perch if the competition levels are not reduced.

The growth of yellow perch can be considered as poor in our study lakes when compared with the observed growth range for the species in North America (Willis et al. 1991). In fact, such growth patterns are similar to those observed by Diana and Salz (1990) for stunted populations in the Great Lakes and by Hayes et al. (1992) for yellow perch populations in lakes dominated by white sucker. Hayes et al. (1992) suggested that competitive interactions between white sucker and yellow perch are strongly asymmetrical, with white sucker being a superior competitor on benthic invertebrates and eventually causing adult yellow perch to switch to alternative prey items such as zooplankton (Hayes et al. 1992). Magnan (1988) found such an asymmetrical competition between white sucker and brook trout, with the latter shifting from zoobenthos to zooplankton when living in sympatry with white sucker. As in the brook trout system (Magnan 1988; Tremblay and Magnan 1991), white sucker is better adapted to and thus more efficient than yellow perch in feeding on benthic organisms. Generally, fish having a ventrally oriented mouth, like white sucker, are more effective bottom feeders, whereas fish with a terminal mouth, like brook trout and yellow perch, are more effective in capturing surface and open-water prey (Webb 1984). Thus, it seems likely that the presence of piscivorous fish in our study lakes did not have a strong enough effect to ease the pressure on the yellow perch (populations were still stunted) because of the presence of a strong competition with white sucker. This

© 2005 NRC Canada

Table 4. Best models predicting the back-calculated length-at-age of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*).

Dependent variable	Independent variable	Standardized estimate	*P*	Partial R^2	Adjusted R^2	*n*	Model *P*
White sucker							
Length-at-age 1	PISC	0.58	0.002	0.37	0.60	18	0.0011
	CACO	0.35	0.042	0.16			
	PEFL	–0.38	0.028	0.14			
Length-at-age 2[a]	PISC	0.71	0.002	0.50	0.47	17	0.0001
Length-at-age 3	PISC	0.58	0.001	0.47	0.72	17	<0.0001
	CACO	0.36	0.018	0.10			
	COCL	0.46	0.004	0.20			
Length-at-age 4	PISC	0.64	0.006	0.40	0.37	17	0.0057
Length-at-age 5	PISC	0.66	0.007	0.44	0.39	15	0.0072
Length-at-age 6	PISC	0.68	0.005	0.47	0.43	15	0.0050
Yellow perch							
Length-at-age 1	PISC	–0.55	0.007	0.30	0.27	23	0.0067
Length-at-age 2	PEFL	0.63	0.004	0.39	0.36	19	0.0042

Note: Eight lake morphometric variables were used as independent variables in the analysis together with the relative biomass (BPUE) of piscivorous fish (PISC) and of five other major fish taxa: CACO, white sucker; COCL, white lakefish (*Coregonus clupeaformis*); PISC, northern pike (*Esox lucius*) plus walleye (*Sander vitreus*); PEFL, yellow perch. All stepwise regressions were significant after the sequential Bonferroni correction. Partial R^2 was calculated as the standardized regression coefficient times the correlation coefficient between the dependent variable and this independent variable (Tabachnick and Fidell 2001).

[a]The dependent variable was transformed into ranks to homogenize the variance (Quinn and Keough 2002).

Table 5. Results of linear mixed models explaining variation in the log weight of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*).

(*a*) Type 3 test of fixed effects.

	White sucker			Yellow perch		
Effect	df	*F*	*P*	df	*F*	*P*
GROUP	2,14	47.7	<0.0001	2,21	25.7	<0.0001
log TL	1,14	93 998.4	<0.0001	1,21	148 844.0	<0.0001
log TL × GROUP	2,14	62.4	<0.0001	2,21	30.8	<0.0001

(*b*) Least square means log weight ± 1 SE.

Group	25th percentile[a]	50th percentile	75th percentile	25th percentile	50th percentile[b]	75th percentile[c]
I	1.74±0.01*a*	1.91±0.01*a*	2.35±0.01*a*	0.75±0.01*a*	0.87±0.01*a*	1.18±0.01*a*
II	1.79±0.01*b*	1.97±0.01*b*	2.43±0.01*b*	0.77±0.01*a*	0.89±0.01*a*	1.21±0.01*a*
III	1.79±0.01*b*	1.96±0.01*b*	2.42±0.01*b*	0.78±0.01*a*	0.91±0.01*a*	1.24±0.01*a*

Note: Adjusted weights (least square means) for the three lake groups were calculated at the 25th, 50th, and 75th percentiles of the independent variable (i.e., log TL, see text). The 25th, 50th, and 75th percentiles of log TL correspond to 180, 205, and 286 mm, respectively, for white sucker and 84, 92, and 117 mm, respectively, for yellow perch. Least square mean values with the same letter are not significantly different after the sequential Bonferroni correction. A total of 1270 white sucker and 2006 yellow perch were included in these statistical analyses.

[a]I versus III: $P = 0.012$.

[b]I versus III: $P = 0.049$.

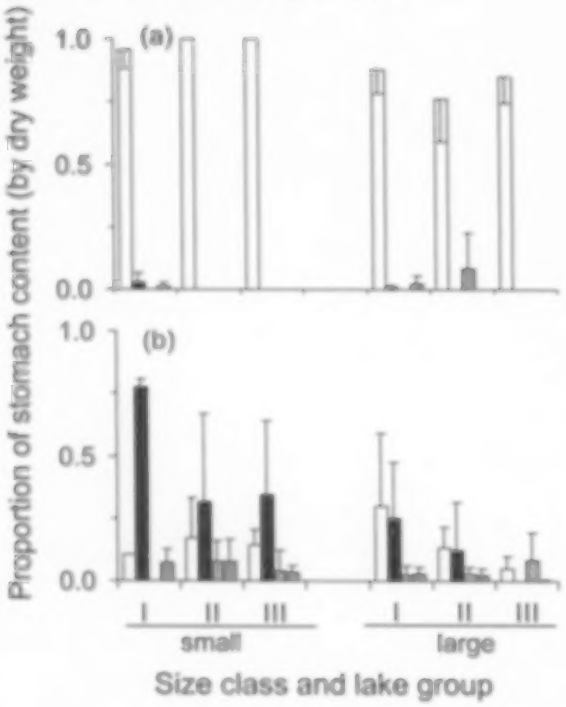
[c]I versus III: $P = 0.0069$.

might also be partially related to the mixed feeding regime of northern pike and walleye in our study lakes. The trophic positions of both walleye and northern pike are variable in the study lakes, suggesting that both species could include benthic invertebrates in their diet (Bertolo et al. 2005). However, stomach content analysis showed that piscivorous individuals were present in all group II and III lakes (A. Bertolo and P. Magnan, unpublished data). The higher growth of white sucker from lake group I compared with groups II and III corroborates the existence of a gradient of piscivory among our study lakes. Northern pike and walleye are in fact known to have strong effects on their prey and, given their different foraging behaviours (northern pike being a "lie-in-wait" predator, while walleye is a "rover" predator; sensu Moyle and Cech 1999), can have complementary effects on prey fish.

Despite the commonness of white sucker and yellow perch in the Canadian Shield, only a few studies have explicitly analyzed the interactions between these two species (e.g., Johnson 1977; Hayes et al. 1992). In contrast with our study, these studies showed that yellow perch responded in the short term to white sucker mass removal by an increase in growth. The differences in stability among these systems could explain this discrepancy, since these populations were

© 2005 NRC Canada

Fig. 2. Proportion of the four functional prey categories (by dry weight) in the stomach contents of two size classes (i.e., small and large) of (*a*) white sucker (*Catostomus commersoni*) (<200 and >200 mm) and (*b*) yellow perch (*Perca flavescens*) (<90 and >90 mm) in the three lake groups: I, no piscivores; II, with northern pike (*Esox lucius*); III, with northern pike and walleye (*Sander vitreus*). Open bars, zoobenthos; solid bars, zooplankton; shaded bars, fish; hatched bars, dipteran pupae.



probably not in a stable state compared with ours. A time lag in the compensatory response of white sucker might explain the short-term positive effects of its removal on yellow perch growth, as was observed by Johnson (1977), an effect likely to be dampened over the longer term. It has been shown that white sucker can rapidly recover to preremoval biomass levels by increasing its growth rate and fecundity after mass removal (i.e., within 3 years after mass removal; Brodeur et al. 2001). Thus, long-term improvement in the growth of stunted yellow perch populations by mass removal of competitors, as suggested by Johnson (1977) and Hayes et al. (1992), seems unlikely when this species co-occurs with white sucker.

In conclusion, our results suggest that the effects of piscivores on the growth of their prey can depend on species interactions and thus on community structure. By reducing the abundance of a prey, piscivores can favour a compensatory growth response of the prey (e.g., white sucker) by a release of intraspecific competition. However, while one of the prey species will profit from the competitive release (e.g., white sucker), the other will not (e.g., yellow perch), owing to interspecific competition with the first prey species. Moreover, differences in habitat use by juveniles of different species may be related to differences in vulnerability to piscivores. The piscivores can thus affect the growth of more vulnerable species (e.g., yellow perch) by restricting juveniles to a suboptimal diet. Given the large overlap in the distribution of these species, such interactions are likely to be common in Canadian Shield lakes and should be considered in the management of yellow perch populations as well as in studies testing the top-down effect of piscivores.

Acknowledgements

We thank the members of the Groupe de Recherche Interuniversitaire en Limnologie (GRIL) who were involved in this research program: Dr. Richard Carignan, Dr. Bernadette Pinel-Alloul, and Dr. Dolors Planas. Stéphane Masson and Isabelle St-Onge provided invaluable field and laboratory assistance and compiled the databases used in this paper. We are also grateful to the many summer assistants who participated in the field and laboratory work. Two anonymous reviewers gave valuable comments on an earlier version of this paper. A. Bertolo was supported by a postdoctoral fellowship from the GRIL and the Canada Research Chair in Freshwater Ecology. This project was supported by grants from the Sustainable Forest Management Network Center of Excellence, the Natural Sciences and Engineering Research Council of Canada, and the Canada Research Chair program to P.M.

References

Abbey, D.H., and Mackay, W.C. 1991. Predicting the growth of age-0 yellow perch populations from measures of whole-lake productivity. Freshw. Biol. **26**: 519–525.

Bertolo, A., Carignan, R., Magnan, P., Pinel-Alloul, B., Planas, D., and Garcia, E. 2005 Decoupling of pelagic and littoral food webs in oligotrophic Canadian Shield lakes. Oikos, **111**(3): 534–546.

Boisclair, D., and Leggett, W.C. 1989*a*. Among-population variability of fish growth: I. Influence of the quantity of food consumed. Can. J. Fish. Aquat. Sci. **46**: 457–467.

Boisclair, D., and Leggett, W.C. 1989*b*. Among-population variability of fish growth: II. Influence of prey type. Can. J. Fish. Aquat. Sci. **46**: 468–482.

Boisclair, D., and Leggett, W.C. 1989*c*. Among-population variability of fish growth: III. Influence of fish community. Can. J. Fish. Aquat. Sci. **46**: 1539–1550.

Brodeur, P., Magnan, P., and Legault, M. 2001. Response of fish communities to different levels of white sucker (*Catostomus commersoni*) biomanipulation in five temperate lakes. Can. J. Fish. Aquat. Sci. **58**: 1998–2010.

Carignan, R., D'Arcy, P., and Lamontagne, S. 2000. Comparative impacts of fire and forest harvesting on water quality in Boreal Shield lakes. Can. J. Fish. Aquat. Sci. **57**: 105–117.

Carpenter, S.R., and Kitchell, J.F. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Chapleau, F., Findlay, C.S., and Szenasy, E. 1997. Impact of piscivorous fish introductions on fish species richness of small lakes in Gatineau Park, Quebec. Ecoscience, **4**: 259–268.

Chen, Y., and Harvey, H.H. 1999. Spatial structuring of length-at-age of the benthivorous white sucker (*Catostomus commersoni*) in relation to environmental variables. Aquat. Living Resour. **12**: 351–362.

© 2005 NRC Canada

Chen, Y., Jackson, D.A., and Harvey, H.H. 1992. A comparison for von Bertalanffy and polynomial functions in modelling fish growth data. Can. J. Fish. Aquat. Sci. **49**: 1228–1235.

Diana, J.S., and Salz, R. 1990. Energy storage, growth, and maturation of yellow perch from different locations in Saginaw Bay, Michigan. Trans. Am. Fish. Soc. **119**: 976–984.

Hayes, D.B., Taylor, W.W., and Schneider, J.C. 1992. Response of yellow perch and the benthic invertebrate community to a reduction in the abundance of white suckers. Trans. Am. Fish. Soc. **121**: 36–53.

Johnson, F.H. 1977. Response of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota lake, 1966. J. Fish. Res. Board Can. **34**: 1633–1642.

Littell, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.D. 1996. SAS system for mixed models. SAS Publishing, Cary, N.C.

Magnan, P. 1988. Interactions between brook charr, *Salvelinus fontinalis*, and non-salmonid species: ecological shift, morphological shift and their impact on zooplankton communities. Can. J. Fish. Aquat. Sci. **45**: 999–1009.

Moyle, P.B., and Cech, J.J. 1999. Fishes: an introduction to ichthyology. Prentice Hall, Englewood Cliffs, N.J.

Olson, M.H., Green, D.M., and Rudstam, L.G. 2001. Changes in yellow perch (*Perca flavescens*) growth associated with the establishment of a walleye (*Stizostedion vitreum*) population in Canadarago Lake, New York (USA). Ecol. Freshw. Fish. **10**: 11–20.

Patoine, A., Pinel-Alloul, B., Prepas, E.E., and Carignan, R. 2000. Do logging and forest fires influence zooplankton biomass in Canadian Boreal Shield lakes? Can. J. Fish. Aquat. Sci. **57**: 155–164.

Paukert, C.P., Willis, D.W., and Klammer, J.A. 2002. Effects of predation and environment on quality of yellow perch and bluegill populations in Nebraska sandhill lakes. N. Am. J. Fish. Manag. **22**: 86–95.

Planas, D., Desrosiers, M., Groulx, S.R., Paquet, S., and Carignan, R. 2000. Pelagic and benthic algal responses in eastern Canadian Boreal Shield lakes following harvesting and wildfires. Can. J. Fish. Aquat. Sci. **57**: 136–145.

Post, J.R., Johannes, M.R.S., and McQueen, D.J. 1997. Evidence of density-dependent cohort splitting in age-0 yellow perch (*Perca flavescens*): potential behavioural mechanisms and population-level consequences. Can. J. Fish. Aquat. Sci. **54**: 867–875.

Power, M., and van den Heuvel, M.R. 1999. Age-0 yellow perch growth and its relationship to temperature. Trans. Am. Fish. Soc. **128**: 687–700.

Quinn, G., and Keough, M. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.

Rudstam, L.G., Green, D.M., Forney, J.L., Stang, D.L., and Evans, J.T. 1996. Evidence of interactions between walleye and yellow perch in New York State lakes. Ann. Zool. Fenn. **33**: 443–449.

SAS. 1999. SAS OnlineDoc version 8 [computer program]. SAS Publishing, Cary, N.C.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

St-Onge, I., and Magnan, P. 2000. Impact of logging and natural fires on fish communities of Laurentian Shield lakes. Can. J. Fish. Aquat. Sci. **57**: 165–174.

Tabachnick, B.G., and Fidell, L.S. 2001. Using multivariate statistics. Harper Collins College, New York.

Tremblay, S., and Magnan, P. 1991. Interactions between two distantly related species, brook trout, *Salvelinus fontinalis*, and white sucker, *Catostomus commersoni*. Can. J. Fish. Aquat. Sci. **48**: 857–867.

Trippel, E.A., and Harvey, H.H. 1987. Abundance growth, and food supply of white suckers (*Catostomus commersoni*) in relation to lake morphometry and pH. Can. J. Zool. **65**: 558–564.

Tyson, J.T., and Knight, R.L. 2001. Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. Trans. Am. Fish. Soc. **130**: 766–782.

Verbeke, G., and Molenberghs, G. 2000. Linear mixed models for longitudinal data. Springer-Verlag, New York.

Webb, P.W. 1984. Body form, locomotion and foraging in aquatic vertebrates. Am. Zool. **24**: 107–120.

Werner, E.E., Gilliam, J.F., Hall, D.J., and Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology, **64**: 1540–1548.

Willis, D.W., Guy, C.S., and Murphy, B.R. 1991. Development and evaluation of a standard weight (Ws) equation for yellow perch. N. Am. J. Fish. Manag. **11**: 374–380.

© 2005 NRC Canada

Using confidence intervals to estimate the response of salmon populations (*Oncorhynchus* spp.) to experimental habitat alterations

Michael J. Bradford, Josh Korman, and Paul S. Higgins

Abstract: There is considerable uncertainty about the effectiveness of fish habitat restoration programs, and reliable monitoring programs are needed to evaluate them. Statistical power analysis based on traditional hypothesis tests are usually used for monitoring program design, but here we argue that effect size estimates and their associated confidence intervals are more informative because results can be compared with both the null hypothesis of no effect and effect sizes of interest, such as restoration goals. We used a stochastic simulation model to compare alternative monitoring strategies for a habitat alteration that would change the productivity and capacity of a coho salmon (*Oncorhynchus kisutch*) producing stream. Estimates of the effect size using a freshwater stock–recruit model were more precise than those from monitoring the abundance of either spawners or smolts. Less than ideal monitoring programs can produce ambiguous results, which are cases in which the confidence interval includes both the null hypothesis and the effect size of interest. Our model is a useful planning tool because it allows the evaluation of the utility of different types of monitoring data, which should stimulate discussion on how the results will ultimately inform decision-making.

Résumé : Il existe beaucoup d'incertitude au sujet de l'efficacité des programmes de restauration des habitats de poissons et il est nécessaire d'avoir des programmes fiables de surveillance pour les évaluer. On utilise généralement des tests statistiques de puissance basés sur des hypothèses traditionnelles pour élaborer les programmes de surveillance; nous pensons que des estimations de l'amplitude des effets et des intervalles de confiance correspondants donnent de meilleurs renseignements, parce que ces résultats peuvent être comparés aussi bien à une hypothèse nulle d'absence d'effet qu'à l'amplitude des effets souhaitée dans, par exemple, des objectifs de restauration. Nous utilisons un modèle de simulation stochastique pour comparer plusieurs stratégies de rechange de surveillance dans le cadre d'un programme d'altération de l'habitat pour changer la productivité et la capacité de support d'un cours d'eau à saumons coho (*Oncorhynchus kisutch*). Les estimations de l'ampleur des effets à partir d'un modèle stock–recrutement d'eau douce sont plus précises que celles obtenus par le relevé de l'abondance des reproducteurs ou de celle des saumoneaux. Les programmes de surveillance imparfaits peuvent donner des résultats ambigus, dans le cas où les intervalles de confiance contiennent à la fois l'hypothèse nulle et l'amplitude des effets désirée. Notre modèle est un outil avantageux de planification parce qu'il permet d'évaluer l'utilité des différentes sortes de données de surveillance, ce qui devrait permettre une discussion sur la manière dont les résultats affecteront en bout de compte la prise de décisions.

[Traduit par la Rédaction]

Introduction

Habitat restoration is being used as a means of reversing declining trends in Pacific salmon (*Oncorhynchus* spp.) abundance in western North America (Roni et al. 2002). There is considerable uncertainty about the effectiveness of these restoration programs, leading some to suggest that restoration activities should be considered experimental and reliable monitoring programs need to be implemented to facilitate learning (Castleberry et al. 1996; Roni et al. 2002).

Detecting changes in the abundance of salmon populations that result from habitat alterations is not easy (Pella and Myren 1974). Interannual variation in abundance and survival of salmon populations is high, and this variation is compounded by the often substantial uncertainty in fish population estimates. Further, abundances can be affected by conditions in the other habitats that salmon use during the completion of their life cycle. Consequently, a variety of studies have been conducted to evaluate the utility of different monitoring schemes, as well as the use of control popu-

Received 6 December 2004. Accepted 11 July 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 28 October 2005.
J18440

M.J. Bradford.[1] Fisheries and Oceans Canada and School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
J. Korman. Ecometric Research Inc., 3560 W 22nd Ave., Vancouver, BC V6S 1J3, Canada.
P.S. Higgins. BC Hydro, 6911 Southpoint Way, Burnaby, BC V3N 4X8, Canada.

[1]Corresponding author (e-mail: mbradfor@sfu.ca).

 doi: 10.1139/F05-179 © 2005 NRC Canada

lations with similar life histories to improve analysis of habitat changes on affected populations (e.g., Bradford 1994; Williams 1999; Paulsen and Fisher 2003).

Most studies have used statistical power analysis to evaluate monitoring protocols for habitat or population changes (e.g., Pella and Myren 1974; Hinrichsen 2001). In Monte Carlo simulations, power is usually the proportion of trials in which a statistical test on the simulated data is deemed "significant", for example, when a t test of mean abundances before and after a habitat change yields $P < 0.05$ for the null hypothesis of no change. The statistical power of monitoring juvenile (Ham and Parsons 2000) and spawner (Pella and Myren 1974; Korman and Higgins 1997) abundance and adult stock–recruit parameters (Hinrichsen 2001) has been considered. The general result from these analyses is that the power to detect changes is often low. However, the different metrics have not often been compared in a single framework to determine if any method is superior to the other (but see Paulsen and Fisher 2003).

The appropriateness of the standard hypothesis-testing framework in environmental and ecological monitoring has been the subject of a lively debate in recent years (e.g., Stewart-Oaten et al. 1986; Harlow et al. 1997); this debate has also occurred in the medical and psychometric literatures (e.g., Smith and Bates 1992; Smithson 2003). One of the contentious issues is the distinction between statistical significance, which is the rejection of the null hypothesis, and the affirmation of an effect of biological or environmental importance (Johnson 1999). Comparisons with only the null hypothesis (in this case, of an effect size = 0) are the basis of traditional power analysis, but the statistical rejection of the null hypothesis provides no direct evidence of the magnitude of the estimated effect or its precision (McBride et al. 1993).

Steidl et al. (1997) and others assert that confidence intervals rather than dichotomous statistical tests should be used to design environmental monitoring programs or ecological investigations. They propose that the confidence intervals be compared with both the null hypothesis and a biologically relevant effect size (such as a management target), allowing the investigator to determine whether the uncertainty around the results includes either or both of these reference points. This approach makes fuller use of the data and more likely emulates the situation that the analyst or technical committee is faced with in reviewing real data at the end of a monitoring program.

In this paper, we used the confidence interval approach in simulation studies to compare alternative monitoring strategies for a habitat alteration that would produce a change in the productive capacity of a salmon-producing stream. This study was motivated by requests for assistance in the design of effective monitoring strategies to evaluate changes in flow regimes in several regulated rivers in southern British Columbia. However, our results can be generalized to any large-scale restoration activity such as those affecting water quality or quantity, biotic manipulations, or extensive physical habitat alterations.

We were posed the usual questions for this sort of analysis: (*i*) What should be monitored? (*ii*) How long will it take? (*iii*) How intensive does the monitoring program have to be? (*iv*) How small an effect will be detectable? We considered three methods to assess the response of a salmon population to a habitat change: monitoring smolt abundance, monitoring spawner abundance, and an evaluation of the changes in the smolt–spawner relation (the freshwater stock–recruit relation). We did not consider changes in the adult stock–recruit relation because the reconstruction of recruits in small salmon populations is not possible when most fish are caught in mixed-stock fisheries.

We tried to emulate the task of a decision-maker at the conclusion of a habitat manipulation experiment. We followed Steidl et al. (1997) and compared the estimated effect (using confidence intervals) with both the null hypothesis of no change in fish abundance and an effect size of interest to managers. In our context, the effect size of interest is the increase in productivity posited at the beginning of the experiment. Water management decisions are sometimes made on the basis of models that attempt to predict the relationship between flow, habitat, and fish populations, and these predictions form the basis for evaluating potential benefits to fish against alternative uses for the water. Because the competition among potential users of the water is often great, we attempted to emulate the case in which a goal of the monitoring program was to determine if the flow changes resulted in the increase in fish production that was predicted, a priori, by the habitat modelling.

Methods

Modelling approach

We used the "operating model" approach (Hilborn and Walters 1992, pp. 237–239) to evaluate monitoring schemes for habitat experiments. We developed a stochastic population model based on the biology of coho salmon (*Oncorhynchus kisutch*) and an estimation scheme that simulated a sampling and analysis program. Monte Carlo simulation was used to characterize the expected range of outcomes of these experiments.

The coho model had two stages simulating the freshwater and marine stanzas of the life cycle. We assumed that seaward migration occurred as age-1 smolts only and all juveniles spent 1.5 years in the ocean before returning to spawning areas to complete a 3-year life cycle. The number of returning spawners is predicted from smolt abundance by assuming a constant density-independent survival rate that combined the effects of natural and fishing mortality. The two-staged model for the coho salmon life cycle was

$$(1) \qquad \mathrm{Sm}_t = (1 + H_t)\frac{\alpha \cdot \mathrm{Sp}_{t-2}}{\beta + \mathrm{Sp}_{t-2}} \cdot e^{v_t}$$

and

$$(2) \qquad \mathrm{Sp}_{t+1} = \mathrm{Sm}_t \cdot \mathrm{MS} \cdot e^{\mu_t}$$

where eq. 1 is a Beverton–Holt stock–recruitment (SR) relationship to predict the abundance of smolts (Sm) as a function of parent spawner (Sp) abundance, t is the year of entry into the ocean, α and β are parameters of the SR relationship, and v_t is a normally distributed process error term with mean 0 and standard deviation (SD) = σ_v (i.e., $v_t = N(0, \sigma_v)$). The Beverton–Holt function emulates the strong density-dependent survival often observed for stream-rearing juveniles (Bradford et al. 2000). Here α/β is the number of

© 2005 NRC Canada

smolts produced per spawner at low spawner abundance; the equilibrium number of smolts is $\alpha - \beta/MS$. The H parameter in eq. 1 simulates the effects of habitat improvement and was set to 0 for the pretreatment period and >0 after the habitat manipulation. Equation 2 predicts the number of returning spawners based on a constant marine survival rate (MS) and a normally distributed process error term μ_t with mean 0 and SD = σ_μ. Thus we assumed lognormal process error in both freshwater and marine stages (Bradford 1995).

In our formulation of the effects of habitat improvements on productivity, we assumed a proportional increase in both the slope and asymptote of the smolt–spawner relation (Fig. 1). We assumed this because we do not know the exact mechanism by which a change in flow might affect fish production. However, in a life history based derivation of the Beverton–Holt function, Walters and Korman (1999) found that both the slope and asymptote were sensitive to changes in physical factors affecting foraging success or the risk of predation. If more specific information were available on the linkage between the habitat manipulation and fish production, eq. 1 could easily be modified accordingly.

The response of the model population to a habitat change will depend on the population's production parameters. When productivity at low abundance is high, the change in the equilibrium smolt abundance is similar to the magnitude of the habitat change and the population is expected to respond quickly (Fig. 1*a*). By contrast, when productivity is low, the equilibrium smolt abundance prior to habitat change might be on the ascending part of the posttreatment Beverton–Holt curve (Fig. 1*b*). Consequently, the change in equilibrium population size after habitat improvements is larger and can be larger than the proportional increase in habitat. However, because of the lower productivity, the population may take a number of generations to reach the new equilibrium abundances (Korman and Higgins 1997), which may affect the capability of a monitoring program to detect the effects of a habitat change.

To generate "observed" data, we assumed that spawner and smolt abundance was estimated by field programs with multiplicative measurement errors (Korman and Higgins 1997):

$$\hat{S}m_t = Sm_t \cdot e^{\psi_t} \quad (3)$$

$$\hat{S}p_t = Sp_t \cdot e^{\phi_t} \quad (4)$$

where ψ_t and ϕ_t are normally distributed error terms with mean 0 and SD = σ_ψ and σ_ϕ, respectively.

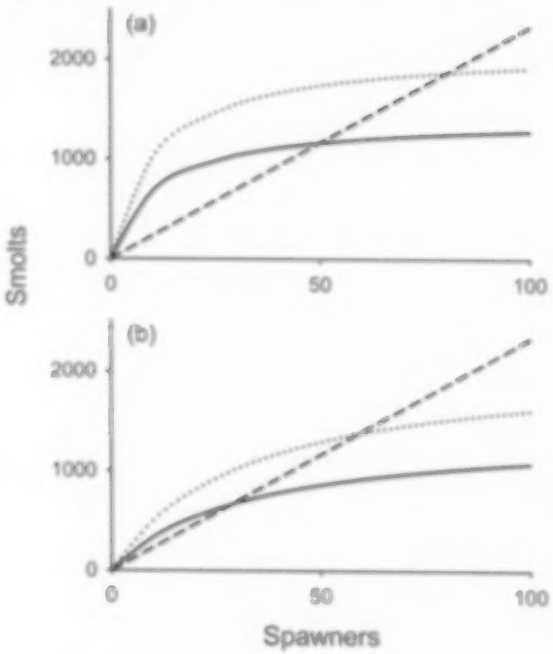
Most of our analyses were conducted using a BA (before–after) design, but we also used a BACI (before–after, control–impact) design, which includes a control population. BACI experiments are useful when there is common variation in population processes that can "controlled" or explained by the use of unaffected populations (Stewart-Oaten et al. 1986). In the case of coho salmon survival, both freshwater and marine components could share a regional factor driven by large-scale climate processes. In addition, ocean survival is often autocorrelated because of decadal-scale variation in ocean conditions (Coronado and Hilborn 1998).

For the BACI design, we simulated a control population that used the same model structure and baseline parameters as the treatment population. To simulate covariation between the control and treatment population caused by ocean conditions experienced by both populations, we first simulated annual values of a common marine environment variable (ξ) that was $N(0,1)$ and included a first-order autoregressive process with a lag-1 correlation coefficient (ρ). We then created marine survival deviations for the treatment and control populations (μ_i, where i refers to one of the two populations) for use in eq. 2 as

$$\mu'_{i,t} = \sigma_\mu\left(\sqrt{(1 - r_m^2)} \cdot \zeta_{i,t} + r_m \cdot \xi_t\right) \quad (5)$$

where r_m is the correlation between the common marine environment and each stock-specific marine survival rate and ζ is a $N(0,1)$ random variable that simulates survival variation unrelated to the common marine signal for year t. Equation 5 creates survival deviations that are both autocorrelated and correlated across treatment and control populations.

Fig. 1. Hypothetical spawner-to-smolt stock–recruitment curves to show the theoretical effects of habitat enhancement on equilibrium population size. In each panel, the solid line is the baseline relationship, and the dotted line represents a 50% increase in production resulting from habitat change (H = 0.5 from eq. 1). The broken line is the replacement line based on a 4.3% smolt-to-adult survival rate. The intersection of the replacement line and the recruitment curve is the equilibrium population size. (*a*) Productivity at low abundance is high (α/β = 129) and the expected increase in equilibrium smolt abundance resulting from habitat change is 61%, slightly more than the predicted habitat increase. (*b*) A lower productivity population (α/β = 44) showing that the increase in population size is 106%, more than twice the gain in habitat.



© 2005 NRC Canada

Table 1. Statistics for 13 coho salmon (*Oncorhynchus kisutch*) populations from coastal streams of western North America from Bradford et al. (2000).

Population	n	α	β	SD_v	Productivity	Marine survival	SD_μ
Big Beef	18	1905	25.2	0.31	75	0.038	0.75
Black Creek	12	3264	54.2	0.45	60	0.029	1.09
Carnation	26	1401	12.2	0.29	115	0.033	0.94
Dechutes	17	5355	217.0	0.34	25	0.047	0.93
Deer Creek	13	1416	14.9	0.24	95	0.026	0.52
Flynn Creek	13	465	3.4	0.61	139	0.049	1.02
Hooknose	13	865	1.8	0.27	471	0.059	0.72
Hunts	11	1172	28.4	0.66	41	0.083	0.87
Minter	11	1889	5.8	0.24	325	0.037	0.65
Needle Branch	12	349	5.2	0.36	67	0.088	1.08
Nile	9	1032	21.1	0.17	49	0.065	0.49
Skykomish	11	3438	31.7	0.14	109	0.043	0.66
Snow	15	1767	45.7	0.36	39	0.039	1.94
Percentiles							
20th				0.24	44	0.034	0.66
Median				0.31	75	0.043	0.87
80th				0.42	129	0.069	1.06

Note: α and β, estimates of parameters of the Beverton–Holt spawner-to-smolt relationship (eq. 1); SD_v, estimates of log-residual variation in the smolt–spawner data; productivity α/β, the ratio of smolts to spawner at very low spawner abundance; marine survival, the proportion of smolts that return to spawn the following year as adults; SD_μ, the interannual variation in log-transformed marine survival.

We used the same approach for the freshwater survival deviations with a correlation parameter r_{fm}. We did not model autocorrelated variation in freshwater survival rates.

Model parameterization

We used spawner and smolt abundance data from 15 coho populations from coastal streams along the western slope of North America from Bradford et al. (2000) to estimate the range of reasonable parameter values for the model (Table 1). Estimates of α, β, and σ_v were derived for each of the stocks by fitting the model using a maximum likelihood approach assuming lognormal error (Hilborn and Mangel 1997). The fitting procedure failed to generate reasonable estimates of stock productivity for two of the 15 stocks in which smolt abundance appeared independent of spawner abundance, even at low spawner abundance (Big Qualicum and Bingham), and those estimates were not used in the calculation of summary statistics used to parameterize model simulations.

In all model runs, the median value for α (1416 smolts·km^{-1}) was used. Population productivity at low abundance was varied, and we used values based on the 20th (44 smolts·spawner^{-1}), median (the baseline, 75 smolts·spawner^{-1}), and 80th (129 smolts·spawner^{-1}) percentile from the 13 productivity estimates to span the potential range across streams. We used the median value for environmental variation in smolt production ($\sigma_v = 0.3$).

Marine survival rates were computed as the logarithmic mean of Sp_{t+1}/Sm_t and therefore included the effects of fishing mortality. Estimates of σ_μ for each stock were from log-transformed survival rates. Most of the spawner and smolt abundance estimates were made from fences or weirs, so we assumed that the variance in marine survival rates and residuals around the spawner-to-smolt recruitment relationships represents process error alone. In our baseline simulations, we used the median values for marine survival (4.3%) and process error in marine survival ($\sigma_\mu = 0.9$).

Values for observation error were drawn from a survey of the literature. Mark–recapture programs for smolts have yielded values of σ_ψ of 0.1–0.2 (e.g., Thedinga et al. 1994; Miyakoshi et al. 1998), although in some cases larger values have been found (Roper and Scarnecchia 1999; Mantyniemi and Romakkaniemi 2002). Similar ranges have been found for adult estimation programs (Cousens et al. 1982; Korman et al. 2002). For convenience we used the same value for both smolt and spawner estimation errors in most simulations. We used a value of 0.2 (i.e., $\sigma_\psi = 0.2$, $\sigma_\phi = 0.2$) to represent a robust mark–recapture program in our baseline simulations, but we also used values of 0.0, 0.1, and 0.4 to evaluate the performance of perfect, enhanced, and relatively poor monitoring programs, respectively.

The control stream used in the simulated BACI design had the same population parameters and sampling precision as the treatment population. We also required estimates of the correlation in survival rates among populations that would be the result of a common environmental effect that both populations might experience. For smolt-to-adult survival rates, we used data from one wild and five hatchery populations from Georgia Strait, British Columbia, and found the average $R^2_{obs} = 0.6$ (data from Simpson et al. 2003). We set $r_m = 0.88$ in eq. 5 to generate stock covariation that had an average value equal to the observed covariation among stocks in the Georgia Strait $\left(r_m = \sqrt[4]{R^2_{obs}}\right)$. The autocorrelation in the common marine variable (ρ) was set to 0.8. Application of eq. 5 with $\rho = 0.8$ resulted in smolt-to-adult survival rates

© 2005 NRC Canada

that have serial autocorrelation values of about 0.6, which is similar to empirical data for the Georgia Strait populations.

Estimates of the correlation of freshwater survival rates among populations were adapted from Bradford (1999), who found that the maximum squared Pearson's correlation coefficients for coho smolt abundances for streams within ~30 km was 0.2. We assumed that variation around the smolt–spawner relation would have the same degree of covariation and thus set $r_{ln} = 0.67$.

Analysis of simulated data

We initiated each simulation by first running the model population for 10 years before beginning the experiment. The model then simulated population abundance for a specified number of years, with the change in habitat occurring midway through the trial. A smolt or spawner estimate was considered part of the treatment group if the cohort had experienced enhanced freshwater conditions during its second year (as a rearing juvenile).

Following each trial we estimated the effect of the habitat change from the time series of estimated smolt and spawner data. Geometric mean spawner–smolt abundances during the pre- and post-treatment periods were computed from log-transformed data, and the difference in the means was calculated. We computed confidence intervals (CI) for the mean difference in log-transformed smolt and spawner abundances before and after the habitat change for each Monte Carlo trial. Standard formulae based on the t distribution were used. We calculated 80% confidence limits based on our interpretation of the stakeholders' perception of the risks associated with the use of different confidence intervals (see Mapstone (1995) for a discussion). The proportional change in smolt or spawner abundance after the habitat change was calculated from the geometric mean abundances.

The change in the freshwater stock–recruit relation resulting from habitat change was evaluated by fitting the Beverton–Holt function and estimating H for the posttreatment period with a nonlinear iterative search procedure. To speed the searching process, initial values for α and β parameters were the baseline input parameters for the model. If the nonlinear search procedure failed to produce reasonable estimates for H (negative values or values greater than 10), then the trial was rejected and an estimation failure was recorded. Likelihood profiles were used to estimate 80% confidence intervals for H (Hilborn and Mangel 1997). For each parameter set, we ran 1500 Monte Carlo trials and summarized the trial-specific point estimates of the proportional change in spawner or smolt abundances and H with box-and-whisker plots.

To summarize the confidence interval results, we then devised a simple algorithm to emulate the process that a manager might use to evaluate the results of a habitat experiment. This algorithm was based on the comparison of the CI for the estimated effect with two reference points: the null model of no effect and the effect size of interest specified a priori by the managers. For the smolt and spawner measures, the latter reference point was derived from the mean abundance during the control period multiplied by the expected increase in productive capacity ($1 + H$). Here we are trying to emulate the case where the spawner-to-smolt stock–recruitment parameters are unknown before the experiment begins, so the exact response of the population to the habitat change (as indicated in Fig. 1) is unknown. We used a default assumption that the predicted population increase will be directly proportional to the habitat change. For the smolt–spawner analysis, confidence intervals for the estimated H were compared directly with 0 (no effect) and with the predicted value for H.

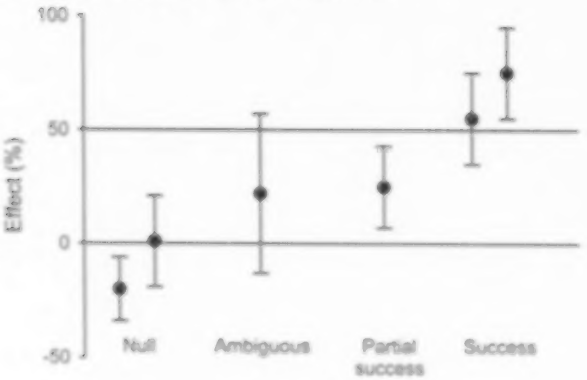


Fig. 2. Example of the scheme used to categorize baseline simulation results based on the comparison of the confidence intervals with the null hypothesis of no effect and the hypothesized 50% increase in habitat. In our analyses, the relatively rare partial success trials were classed as successful.

We categorized individual simulation runs based on whether the CI included the null hypothesis or the predicted increase in abundance (Fig. 2) in one of three categories. (1) Null: consistent with the null hypothesis. Here the CI includes the null case but not the management objective. This category also included the very rare occurrences of a large negative effect that resulted in the upper bound of the CI being below the null. (2) Ambiguous: CI includes both the null and the predicted values. (3) Successful: CI includes the management objective but not the null. We also included the few trials in which the increase was much larger than expected and the lower bound of the CI was above the predicted value. A fourth category that included cases in which the CI was between the null and the predicted levels (a partial success) was also tallied, but occurrences of this were rare so we included them in the successful category.

The major difference between evaluating experimental designs using confidence intervals rather than hypothesis tests is the identification of a management or biological goal in addition to the null hypothesis. Our successful category is equivalent to power with a specified type I error rate, but our approach identifies those nonsignificant trials that are potentially consistent with the management objective of increased abundance, as well as the null hypothesis. This additional information is potentially useful for forecasting the type of information that will be generated at the end of the trial and for thinking about how the results will be interpreted.

For the BACI comparisons, we computed the annual values for the difference in log-transformed smolt or spawner abundance between the control and treatment populations and then averaged those over the control and treatment periods. In the model runs that included autocorrelated marine survival, we adjusted the confidence intervals for spawners

© 2005 NRC Canada

Fig. 3. Box-and-whisker plots showing the distribution of point estimates of the estimated effect size for an experiment with a 50% increase in habitat and the baseline parameters. In each case, the box is the interquartile (25th to 75th percentiles) range, with the median indicated by the horizontal line. The vertical lines are the 90% range. In this and all following plots, the horizontal axis is the total experiment length, divided evenly between control and treatment periods. Results are shown for the three different indicators: smolts, open bars; spawners, hatched bars; change in spawner-to-smolt relationship (H), shaded bars.

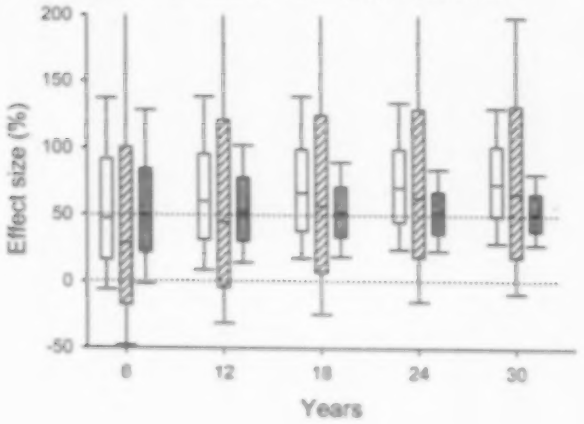
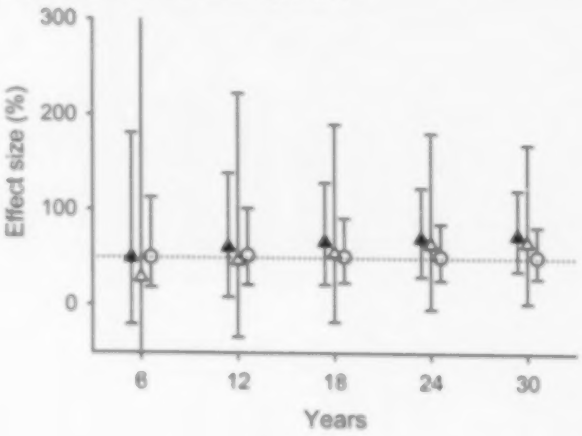


Fig. 4. Average 80% confidence intervals for each indicator. For smolts and spawners, confidence intervals are expressed as the percent increase over the control period; symbols indicate the average effect size over all trials. The modelled increase in habitat is indicated by the broken line. Smolts, ▲; spawners, △; change in spawner-to-smolt relationship (H), ○.



because intervals calculated using standard formulae are too small (Bence 1995). Annual abundances of spawners are autocorrelated in the among-stock correlated survival rate scenario because spawner abundances are directly affected by autocorrelated smolt-to-adult survival rates. We corrected the CI for spawners using the ad-hoc procedure from Bence (1995) of multiplying the standard error used in the calculation of the confidence interval by a correction factor $k = [(1 + \rho)/(1 - \rho)]^{0.5}$, where ρ is an estimate of the autocorrelation (we used $\rho = 0.6$). Smolt abundances were not serially correlated because of the strong filtering effect of the smolt–spawner relation that removes most of the influence of spawner abundance on smolt production, so we did not apply this correction. Monte Carlo trials for the BACI analysis were categorized like those from the BA analysis.

The BACI design can also be incorporated into the estimation of the change in the smolt–spawner relation, but the resulting model contains a much larger number of parameters (two sets of Beverton–Holt parameters, H, and common year effects). Because the degree of covariation in freshwater survival is relatively small, we considered that the benefits of using the BACI approach to estimate the smolt–spawner parameters would be relatively low and did not attempt the more complex fitting procedure here.

Results

Baseline case

In our baseline case, the habitat-related increase in productivity was set at 50% (i.e., $H = 0.5$), but the combined effects of process and observation error resulted in considerable trail-by-trial variation in the point estimates of the response of the population (Fig. 3). As expected, this variation became smaller as the duration of the trials increased. The point estimates of effect size were most variable for the spawner indicator, with some very extreme estimates being produced. The smolt–spawner analysis (H) produced the least variable results.

Bias caused by the lag in the population response to the habitat change varied among indicators (Fig. 3). For both spawners and smolts, the median of the estimated effect sizes across trials increased with increasing duration of the trial because the influence of the population lag diminished as the number of treatment years increased. Estimates of H from the smolt–spawner relation were not biased. Median estimates of the increase in smolts and spawners were greater than 50% for the longest experiments because of the shift in population equilibrium noted in Fig. 1.

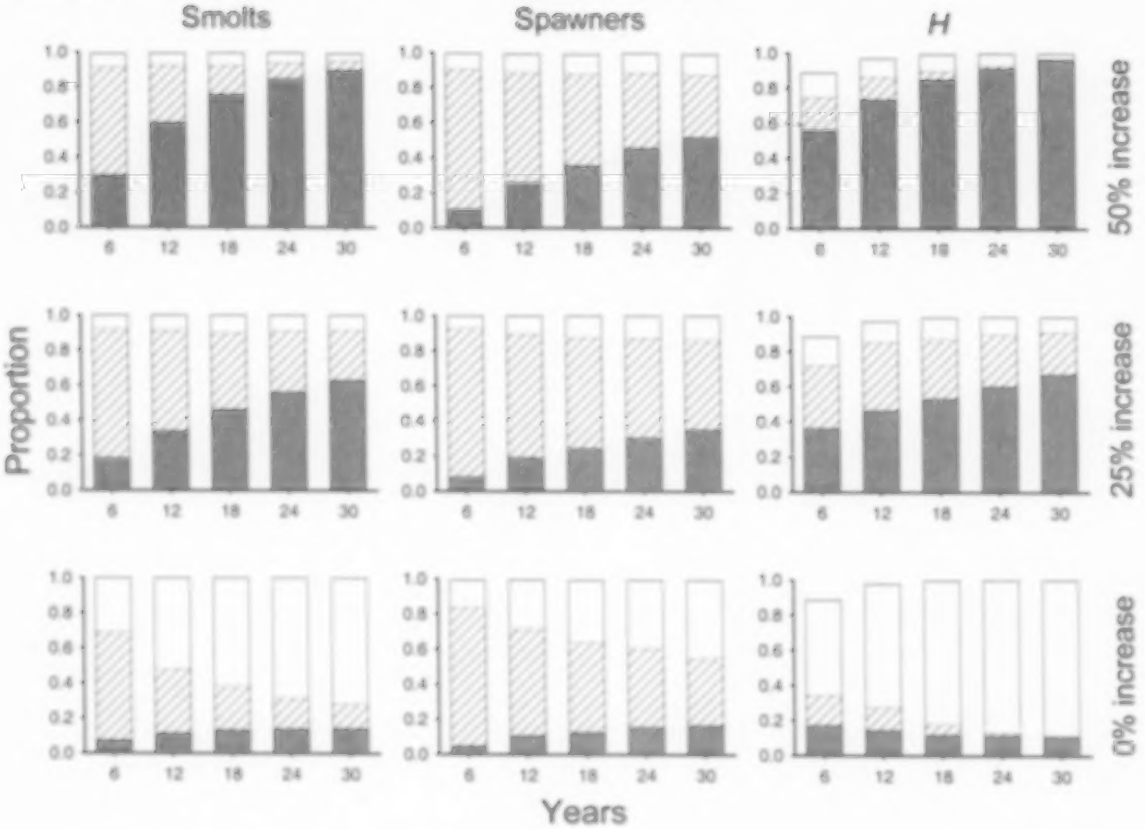
Confidence interval analysis

Each simulation resulted in a point estimate of the effect size (summarized in Fig. 3) and an associated confidence interval. To summarize the typical uncertainty around the point estimates, we calculated the average width of confidence intervals across trials for each indicator and experiment length. On average, confidence intervals were widest for the spawner indicator and narrowest for H (Fig. 4). Confidence intervals decreased in width asymptotically as the duration of trials increased.

In the baseline scenario, the proportion of simulation trials that was sorted into the null category was low (3%–15%) for all three indicators and was largely independent of experiment length (Fig. 5, upper row). Ambiguous results were common for the shorter experiments using the smolt and spawner indicators, but their occurrence diminished for the longer trials as more cases were classed as successful. The model-based approach of estimating H generally outperformed the other measures in recording success rates ≥70% for experiments of 12 years or longer. Estimation failures for

© 2005 NRC Canada

Fig. 5. The proportion of simulation trials sorted in three classes based on their confidence intervals (CI). Shown are results for the case in which the increase in productivity was 50% (i.e., true $H = 0.5$, upper row), the case in which the actual increase was 25% (true $H = 0.25$, middle row), and the case in which there was no actual increase in productivity (true $H = 0$, lower row). For the upper and lower rows, the CIs were compared with the a priori management hypothesis of $H = 0.5$. For the middle row, the hypothesized value of H was 0.25. In each stacked bar, the proportion of successful trials is indicated by the shaded bar, the proportion of ambiguous cases is indicated by the hatched bar, and the proportion classified as null is indicated by the open bar. For the spawner-to-smolt measure (H), some bars do not sum to 1.0 because of a small proportion of fitting failures.



H occurred in 15% of cases for the 6-year trials but were relatively rare otherwise.

Alternative population responses

We simulated the scenario in which the hypothesized effect and the actual population response was 25%, half the baseline case. In all cases, the proportion of null cases was relatively low, but ambiguous results were much more common than the baseline results, especially for the shorter experiments (Fig. 5, middle row).

Finally, we ran a trial in which the hypothesized effect was a 50% increase, but in fact, there was no actual habitat effect (Fig. 5, lower row). This simulated the situation in which the habitat change was completely ineffective. For the smolt and smolt–spawner indicators, there were a large proportion of null results, indicating the population response was correctly identified.

Sensitivity analyses

We ran simulations using the baseline parameter set and varied key parameters individually in sensitivity analyses. To succinctly summarize our findings, we tabulated the proportion of trials classified as successful for 12-year experiments only. The general trends for other experiment lengths were similar to those indicated in Fig. 5. We first reran the model with low or high productivity at low abundance and found for the smolt indicator that the occurrence of successful trials was positively associated with productivity (Table 2). A more productive population reached its new equilibrium sooner than a less productive one, which resulted in a higher posttreatment average abundance and an increased proportion of successful experiments. The rate of successful trials was always low for the spawner indicator and unaffected by freshwater productivity. In this case, the relatively high process error in marine survival rates overwhelmed the benefit of a reduced lag time in population response. H was relatively insensitive to differences in freshwater productivity because the lag effect in the abundance response to the habitat alteration is accounted for in the estimation of H.

When the model was run using a lower value for the standard deviation in smolt-to-adult survival (σ_μ of eq. 2), we found that the proportion of successful trials increased for

© 2005 NRC Canada

Table 2. Sensitivity analysis showing the proportion of 1500 trials categorized as successful (12-year experiments) under a range of freshwater stock productivity, marine survival, process error, and measurement error values for smolt- and spawner-based abundance estimates and the estimated change in the spawner-to-smolt relationship (H).

Parameter (baseline values in parentheses)	Value used	Proportion "successful"		
		Smolts	Spawners	H
Baseline case		0.61	0.27	0.74
Low freshwater productivity (α/β = 75)	40	0.46	0.24	0.73
High freshwater productivity (α/β = 75)	140	0.71	0.26	0.68
Low variation in marine survival (σ_v = 0.9)	0.40	0.77	0.44	0.65
Measurement error (σ_v,σ_e = 0.2)				
None	0.0	0.66	0.27	0.87
Low	0.10	0.64	0.27	0.83
High	0.40	0.50	0.26	0.54

the smolt and spawner indicators but decreased by 0.09 (0.74–0.65 = 0.09 in Table 2) for H. This minor decrease was due to the reduction in contrast in spawner abundance resulting from a less variable marine survival rate.

The performance of the smolt and H indicators was somewhat sensitive to measurement error, but a large improvement in performance in H was observed in the low or no measurement error case (Table 2). Measurement error had little effect on the spawner indicator because the magnitude of process error was much greater than the changes in measurement error that were simulated.

H is estimated using both smolt and spawner data so we varied the measurement error associated with each abundance estimate independently (Table 3). We found that H was far more sensitive to measurement error for smolts than for spawners because error in spawner estimates only effects the estimation of H when the true estimates are on the ascending part of the spawner-to-smolt relationship.

Table 3. The proportion of 12-year experiments classified as successful for the estimated change in the spawner-to-smolt relationship (H) as a function of measurement error in the estimates of smolt and spawner abundance.

Smolts (σ_v)	Spawners (σ_e)		
	0	0.2	0.4
0	0.87	0.85	0.80
0.2	0.76	0.74	0.70
0.4	0.56	0.56	0.54

BACI design

When there was no correlation between the survival rates of the control and treated populations, there was a 5%–20% decrease in the proportion of trials classified as successful in the BACI design compared with the simpler BA one (Fig. 6, solid lines). When survival rates were correlated, the BACI and BA designs produced almost identical results for the smolt indicator. For spawners, the BACI design increased the proportion of trials classified as successful by 0.1 to 0.3 (Fig. 6*b*), although the spawner indicator was always inferior to the smolt indicator.

In the baseline case, we assumed only a weak correlation in freshwater survival rates (R^2 = 0.2). When we increased this value to 0.6, we found the proportion successful (12-year experiment) for smolts increased from 0.60 to 0.69, indicating some benefit of the BACI design when both freshwater and marine survival rates are correlated across populations.

Discussion

Our work represents a significant departure from previous analyses of salmonid monitoring designs because we focussed on the information provided by confidence intervals around estimated effect sizes rather than on the more commonly used dichotomous hypothesis tests. In addition, we used a model-based approach to directly estimate the change in freshwater productivity and found that under many circumstances it was superior in performance to monitoring abundances alone.

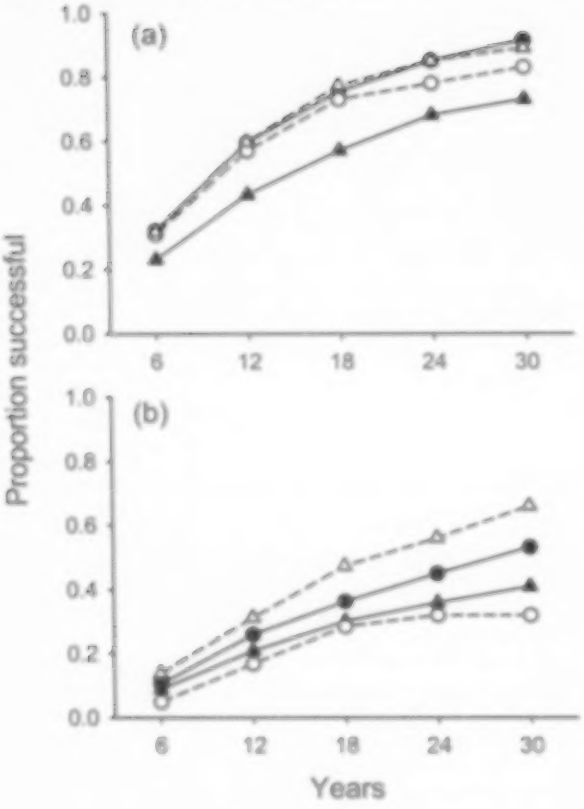
We found that under certain circumstances reasonably informative monitoring programs can be designed. These conditions are (*i*) that the habitat manipulation leads to substantial and immediate increase in fish production, (*ii*) that the experiment last at least 4–6 generations, and (*iii*) that reasonably precise estimates of abundance can be obtained. Departures from these conditions could reduce the quality of information resulting from the experiment.

The stock–recruit model-based approach generally performed well, except in very short trials for which estimation failures were more likely to occur. Estimates of H were unbiased regardless of population productivity or experiment length because the model-based approach accounts for the relationship between parent and smolt abundances and is not biased by lags in the response of the population to habitat changes. The intertrial variation in the estimates of H was lower than the effect size estimates for the abundance indicators, and the confidence intervals for H were narrower than for the other indicators.

Our results for the model-based indicator are potentially optimistic because we are fitting the same model to the data as the one that was used to generate the simulated population trends. That is, we are simulating the situation in which the model for fitting the data has been correctly identified by the analyst both in terms of its overall form (e.g., Beverton–Holt) and in the nature of the effect of habitat change on the smolt production. While the freshwater production dynamics

© 2005 NRC Canada

Fig. 6. Comparison of the before–after (BA; circles) and before–after, control–impact (BACI; triangles) designs. Plots show the proportion of trials classified as successful for (*a*) smolt and (*b*) spawner indicators. Results are shown for the baseline case, in which survival rates were uncorrelated (solid lines and solid symbols), and the case in which marine survival rates were autocorrelated and the annual survival rates of the treatment and control population were correlated for both the freshwater and marine phases (broken lines and open symbols).



of coho salmon are well known (Bradford et al. 2000), the effects of a habitat alteration on model parameters is not, and the wrong choice of the form of the habitat effect could affect estimates of that effect.

We found that smolt abundance measures generally outperformed those based on spawner abundance by providing somewhat less biased and often more precise estimates of the population response to habitat change. In our model the effects of freshwater habitat change on subsequent spawner abundance are masked by the high random variation in smolt-to-adult survival. Although Williams (1999) suggests that the utility of monitoring juvenile migrants or adults will be similar, our results and those of Paulsen and Fisher (2003) clearly show benefits to monitoring juveniles over adults. Monitoring adults will be more successful in cases where the variability in smolt-to-adult survival is significantly lower than in the example we used here.

The successful experiments that we have identified are sensitive to the estimates of population productivity and variability that we used. Estimates of the interannual variation in survival have considerable uncertainty when derived from few data, and this variance will differ among populations (Carey and Keough 2002). We found that the detection of the habitat change for abundance-based indicators was more likely if the population was more productive and more likely for all indicators if survival was less variable. Thus our examples should only be used as rough guides: in most cases, we foresee that a site-specific evaluation will be needed.

We found that ambiguous results, those in which the data are consistent with both the null and hypothesized effects, are highly likely in many scenarios, even for well-planned trials. The likelihood of a management experiment yielding ambiguous results needs to be communicated clearly to managers in advance of embarking on such a program. Such a discussion should lead to a more explicit consideration of how decisions will be made with uncertain data. For example, we have chosen the 80th percentile for our confidence interval analyses, but managers may wish to consider different values, depending on their considerations of the costs and benefits of those decisions. In addition, there is likely merit in considering ancillary information along with fish abundance data. Information on the target species (such as the size, age, and condition, etc., of individuals), data on other trophic levels, changes to the physical habitat, and other attributes of the ecosystem could result in a multidimensional evaluation of whether the treatment produced a satisfactory response.

Our model is useful for determining the effects of changes in the precision of abundance estimates, which ultimately will affect monitoring costs. The impact of measurement error on population statistics depends on the proportion of the total variance attributable to natural process and measurement error. High natural variation in smolt-to-adult survival rates resulted in the spawner indicator being insensitive to the range of measurement error we used. We found that the smolt–spawner analysis was sensitive to measurement error, because the uncertainty in both spawner and smolt estimates enters into the analysis. The sensitivity analysis showed that improvements in the performance of H would be more readily obtained by making smolt estimates as precise as possible. In addition, the rate of fitting failures for the smolt–spawner model increased from 0 to 0.28 for 6-year trials and from 0 to 0.12 for 12-year trials as measurement error was increased from 0.1 to 0.4. Measurement errors are also known to generate bias in parameter estimates from stock–recruit relations (Hilborn and Walters 1992), but we found a maximum 8% positive bias in estimates of H in the high measurement error trials (results not shown). Thus bias resulting from measurement error does not appear to be an issue in our procedure for estimating the effects of habitat change (H).

We did not find the BACI design to be uniformly helpful in improving the precision of monitoring results. Because the test statistic of a BACI design is based on the difference between two estimated abundances (i.e., from the treatment and control streams), the influence of measurement error is greater for the BACI design than for the BA design. Thus the reduction in process uncertainty gained by using a correlated variable has to overcome the loss in precision from the increased measurement error of the test statistic (Loftis et al.

© 2005 NRC Canada

2001). In the case of the smolt estimator, the correlation among freshwater survival rates is low, and the BACI design was, on average, worse than the simple BA approach. The strong covariation in marine survival rates did make the BACI design advantageous for monitoring spawner abundances, although spawner abundance always yielded the least precise results compared with the other measures.

The premise of our work was to find monitoring programs that can estimate the response of the fish population to a change in habitat with sufficient precision to be of utility to decision-makers. Our narrow focus on only biological responses has been called a "statistical" or "scientific" approach, because it does not consider the costs of the experiment or the costs or benefits of future changes to policy resulting from the results of the experiment. In contrast, decision theoretic approaches attempt to explicitly incorporate such values into the experimental design (Walters and Green 1997). Both Walters and Green (1997) and MacGregor et al. (2002) suggest that in some circumstances relatively precise (and usually costly) "scientific experiments" are not warranted for decision-making, especially when the costs of monitoring are high relative to the gains predicted under the new policy.

The decision theoretic approach has its challenges, because the optimal experimental design is contingent on the valuation of costs and benefits (both economically and environmentally), stability in those values over the course of the experiment, and the correct specification of the decision rule that will be used at the end of the trial. Analyses to date have not considered the likelihood that stakeholder and society values will change over the course of a lengthy experiment (Clark 2002), and these could render the chosen experimental design inappropriate if there is a marked change in values or legislation over time or if the relative importance of stakeholder groups shifts in unforeseen ways. One can easily think of examples of changes in values that have occurred over the past two decades: the ecosystem vs. game fish emphasis, increased emphasis on aboriginal issues, and the heightened awareness of species previously not considered to be of interest, such as sturgeon (*Acipenser* spp.) and lamprey (*Lampetra* spp.). It might be possible to include uncertainty in future values in a decision analyses for experimental designs, but the likely outcome of that analysis would be a recommendation for a more detailed monitoring program that would be robust to changes in the management system and valuation scheme.

In contrast, the scientific study design we have elaborated here is not conditional on a complex valuation system, although some values are implicit in the choice of the confidence interval width. A significant benefit that is difficult to account for in the decision theoretic framework is that a reasonably precise estimate of the fish response (with the precision articulated by confidence intervals) can be a valuable contribution to sparse international literature on the effects of habitat alterations (e.g., Castleberry et al. 1996). A statistically weak experiment derived from a valuation approach (e.g., MacGregor et al. 2002) may not be useful in larger scientific context because the inherent lack of precision means that it will not be influential in meta-analyses of similar studies. This could be overcome by explicitly weighting learning (McDaniels and Gregory 2004) in the valuation of monitoring programs so that more precise experiments are viewed more favourably.

In conclusion, well-designed monitoring programs such as those simulated here can be the basis for experimental management; however, creative means for evaluating ecosystem responses to human interventions will be required for scientists to be effective in the eye of decision-makers. The evaluation of habitat manipulations will likely continue to focus on quantifying the benefits to highly valued species for which public policy will support the diversion of economic activities. But our analyses clearly show that we should be prepared for less than compelling results. Thus we anticipate that the assembly of multiple lines of evidence (called "adaptive inference" by Holling and Allen 2002) will be used to evaluate the ecosystem responses to management actions. Perhaps the greatest benefit of experimental management will be to the scientists, managers, and stakeholders who, by being involved in evaluating data, competing hypotheses, and ideas, will be engaged in a process of continuous learning, both in terms of the ecosystem response and in the evolution of the value system upon which decisions are to be made (Clark 2002). This learning will hopefully, in the long-term, lead to policy choices that are based on both scientific information and the values of stakeholders affected by those decisions.

Acknowledgements

We thank John Williams, Ken Newman, Brent Mossop, and two anonymous reviewers for comments on this work. Financial support was provided by BC Hydro.

References

Bence, J.R. 1995. Analysis of short time series: correcting for autocorrelation. Ecology, **76**: 628–639.

Bradford, M.J. 1994. Trends in the abundance of chinook salmon (*Oncorhynchus tshawytscha*) of the Nechako River, British Columbia. Can. J. Fish. Aquat. Sci. **51**: 965–973.

Bradford, M.J. 1995. Comparative review of Pacific salmon survival rates. Can. J. Fish. Aquat. Sci. **52**: 1327–1338.

Bradford, M.J. 1999. Temporal and spatial trends in the abundance of coho salmon smolts from western North America. Trans. Am. Fish. Soc. **128**: 840–846.

Bradford, M.J., Myers, R.A., and Irvine, J.R. 2000. Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates based on freshwater production. Can. J. Fish. Aquat. Sci. **57**: 677–686.

Carey, J.M., and Keough, M.J. 2002. The variability of estimates and its effect on power analysis in monitoring design. Environ. Monit. Assess. **74**: 225–241.

Castleberry, D.T., Cech, J.J., Erman, D.C., Hankin, D., Healey, M., Kondolf, G.M., Mangel, M., Mohr, M., Moyle, P.B., Neilson, J., Speed, J., and Williams, J.G. 1996. Uncertainty and instream flow standards. Fisheries, **21**(8): 20–21.

Clark, M.J. 2002. Dealing with uncertainty: adaptive approaches to sustainable river management. Aquat. Conserv. Mar. Freshw. Ecosys. **12**: 347–363.

Coronado, C., and Hilborn, R. 1998. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. Can. J. Fish. Aquat. Sci. **55**: 2067–2077.

© 2005 NRC Canada

Cousens, N.B.F., Thomas, G.A., Swann, C.G., and Healey, M.C. 1982. A review of salmon escapement estimation techniques. Can. Tech. Rep. Fish. Aquat. Sci. No. 1108.

Ham, K.D., and Pearsons, T.D. 2000. Can reduced salmonid abundance be detected in time to limit management impacts? Can. J. Fish. Aquat. Sci. **57**: 17–24.

Harlow, L.L., Muliak, S.A., and Steiger, J.H. 1997. What if there were no significance tests? Lawrence Erlbaum Assoc. Publishers, Mahwah, N.J.

Hilborn R., and Mangel, M. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, N.J.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Hinrichson, R.A. 2001. High variability in spawner–recruit data hampers learning. Can. J. Fish. Aquat. Sci. **58**: 769–776.

Holling, C.S., and Allen, C.R. 2002. Adaptive inference for distinguishing credible from incredible patterns in nature. Ecosystems, **5**: 319–328.

Johnson, D.H. 1999. The insignificance of significance testing. J. Wildl. Manag. **63**: 763–772.

Korman, J., and Higgins, P.S. 1997. Utility of escapement time series data for monitoring the response of salmon populations to habitat alteration. Can. J. Fish. Aquat. Sci. **54**: 2058–2067.

Korman, J., Ahrens, R.N.M., Higgins, P.S., and Walters, C.J. 2002. Effects of observer efficiency, arrival timing, and survey life on estimates of escapement for steelhead trout (*Oncorhynchus mykiss*) derived from repeat mark–recapture experiments. Can. J. Fish. Aquat. Sci. **59**: 1116–1131.

Loftis, J.C., MacDonald, L.H., Streett, S., Iyer, H.K., and Bunte, K. 2001. Detecting cumulative watershed effects: the statistical power of pairing. J. Hydrol. **251**: 49–64.

MacGregor, B.W., Peterman, R.M., Pyper, B.J., and Bradford, M.J. 2002. A decision analysis framework for comparing experimental designs of projects to enhance Pacific salmon. N. Am. J. Fish. Manag. **22**: 509–527.

Mantyniemi, S., and Romakkaniemi, A. 2002. Bayesian mark–recapture estimation with an application to a salmonid smolt production. Can. J. Fish. Aquat. Sci. **59**: 1748–1758.

Mapstone, B.D. 1995. Scalable decision rules for environmental impact studies: effect size, Type I, and Type II errors. Ecol. Appl. **5**: 401–410.

McBride, G.B., Loftis, J.C., and Adkins, N.C. 1993. What do significance tests really tell us about the environment? Environ. Manag. **17**: 423–432.

McDaniels, T.L., and Gregory, R. 2004. Learning as an objective within a structured risk management decision process. Environ. Sci. Technol. **38**: 1921–1926.

Miyakoshi, Y., Hayano, H., Fujiwara, M., Sugiwaka, K., and Irvine J.R. 1998. Assessment of hatchery origin and wild masu salmon (*Oncorhynchus masu*) smolts in the Masuhoro River, 1996. Sci. Rep. Hokkaido Fish Hatchery, **52**: 1–10.

Paulsen, C.M., and Fisher, T.R. 2003. Detecting survival effects of habitat actions: power analysis applied to endangered Snake River spring–summer chinook (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **60**: 1122–1132.

Pella, J.J., and Myren, R.T. 1974. Caveats concerning evaluation of effects of logging on salmon production in southeastern Alaska from biological information. Northwest Sci. **48**: 132–144.

Roni, P., Beechie, T.J., Bilby, R.E., Leonetti, F.E., Pollock M.M., and Pess G.R. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. N. Am. J. Fish. Manag. **22**: 1–20.

Roper, B.B., and Scarnecchia, D.L. 1999. Emigration of age-0 chinook salmon (*Oncorhynchus tshawytscha*) smolts from the upper South Umpqua River basin, Oregon, U.S.A. Can. J. Fish. Aquat. Sci. **56**: 939–946.

Simpson, K., Chamberlain, M., Fagan, J., Holtby, B., Sweeting, R., and Tanasichuk, R. 2003. Forecast for southern and central British Columbia coho salmon. Can. Stock. Assess. Sec. Res. Doc. No. 2003/102.

Smith, A.H., and Bates, M.N. 1992. Confidence-limit analyses should replace power calculations in the interpretation of epidemiological studies. Epidemiology, **3**: 449–452.

Smithson, M. 2003. Confidence intervals. Sage University Papers Series on Quantitative Applications in the Social Sciences, 07-140. Sage Publications, Thousand Oaks, Calif.

Steidl, R.J., Hayes, J.P., and Schauber, E. 1997. Statistical power analysis in wildlife research. J. Wildl. Manag. **61**: 270–279.

Stewart-Oaten, A., Murdoch, W.W., and Parker, K.R. 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology, **67**: 929–940.

Thedinga, J., Murphy, M., Johnson, S., Lorenz, J., and Koski, K. 1994. Determination of salmonid smolt yield with rotary-screw traps in the Situk River, Alaska, to predict effects of glacial flooding. N. Am. J. Fish. Manag. **14**: 837–851.

Walters, C.J., and Green, R. 1997. Valuation of experimental management options for ecological systems. J. Wildl. Manag. **61**: 987–1006.

Walters, C., and J. Korman. 1999. Linking recruitment to trophic factors: revisiting the Beverton–Holt recruitment from a life history and multispecies perspective. Rev. Fish Biol. Fish. **9**: 187–202.

Williams, J.G. 1999. Stock dynamics and adaptive management of habitat: an evaluation based on simulations. N. Am. J. Fish. Manag. **19**: 329–341.

© 2005 NRC Canada

Ecophysiological determinants of the variation in ^{137}Cs concentrations between and within lacustrine fish populations

Marcus Sundbom and Markus Meili

Abstract: One decade after the Chernobyl fallout, the variability of ^{137}Cs activity concentrations among fish within a Swedish lake was >20-fold based on 1361 individuals from seven species collected continually during 1996–1999. Of the total variability, 64% was due to differences between species but only 7% due to temporal variation, which was 1.3-fold for the whole community and 1.3- to 2-fold for population means. Contamination increased with body size (0.6- to 6-fold) and decreased with body condition in most species (1.3-fold). Body size and time together accounted for about half of the total variation within populations. Fish ^{137}Cs was related to differences in feeding ecology, both between and within populations. Biomagnification factors ranged from 2.4 to 5.8. Contamination was highest in piscivorous populations and individuals, intermediate in herbivores and zooplanktivores, and lowest in fish specialized in benthic invertebrates despite their association with contaminated sediments. The ^{137}Cs variance within populations was not correlated with their niche width but moderately positively correlated with fish trophic position and strongly positively correlated with functional omnivory (diversity in prey ^{137}Cs). We conclude that individual resource specialization is an important source of variation in ^{137}Cs concentrations within fish populations.

Résumé : Une décennie après les retombées de Chernobyl, les concentrations de l'activité du ^{137}Cs chez les poissons d'un lac suédois varient par un facteur de >20 fois, d'après un inventaire de 1361 individus appartenant à sept espèces fait régulièrement entre 1996–1999. De cette variabilité totale, 64 % est due aux différences entre les espèces et seulement 7 % à la variation temporelle qui correspond à un facteur de 1,3 pour toute la communauté et de 1,3 à 2 pour les moyennes des populations. La contamination augmente en fonction de la taille corporelle (d'un facteur de 0,6 à 6) et décroît avec la condition corporelle chez la plupart des espèces (d'un facteur de 1,3). Ensemble la taille corporelle et le temps expliquent environ la moitié de la variation totale dans les populations. Les concentrations de ^{137}Cs chez les poissons sont fonction des différences d'écologie alimentaire, tant à l'intérieur d'une même population que d'une population à une autre. Les facteurs de bioamplification varient de 2,4 à 5,8. La contamination est maximale chez les populations et les individus piscivores, intermédiaire chez les herbivores et les zooplanctonophages et minimale chez les poissons spécialisés pour se nourrir du benthos, malgré leur association avec les sédiments contaminés. La variance du ^{137}Cs au sein d'une population n'est pas fonction de la largeur de la niche, mais elle est en corrélation positive moyenne avec le rang trophique du poisson et en forte corrélation positive avec l'omnivorie fonctionnelle (diversité du ^{137}Cs dans les proies). Nous en concluons que la spécialisation individuelle pour les ressources est une source importante de variation des concentrations ^{137}Cs dans les populations de poissons.

[Traduit par la Rédaction]

Introduction

The radioactive Cs isotopes ^{134}Cs and ^{137}Cs are not naturally occurring in the biosphere. Nevertheless, radiocesium is today a global pollutant because of nuclear bomb tests, accidental releases, and continual routine emissions. Freshwater biota readily accumulates radiocesium, implying potential health hazards for people. For this reason, radiocesium in aquatic ecosystems has been studied for decades, especially the long-lived ^{137}Cs (half-life 30.2 years). The interest in modeling the fate of ^{137}Cs in lakes and watersheds has been renewed since the Chernobyl accident in 1986. In addition, the use of radiocesium as a tracer or research tool has increased dramatically, including bioenergetics (Tucker and Rasmussen 1999; Gingras and Boisclair 2000), trophic dynamics (Meili 1991; Sherwood et al. 2002), and migration of fish (Tucker et al. 1999). Such applications typically employ a bioenergetic mass-balance

Received 11 January 2005. Accepted 2 July 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 29 October 2005.
J18495

M. Sundbom.[1,2] Department of Limnology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 20, SE-75236 Uppsala, Sweden.
M. Meili. Department of Applied Environmental Science, Stockholm University, SE-10691 Stockholm, Sweden.

[1]Corresponding author (e-mail: marcus.sundbom@itm.su.se).
[2]Present address: Department of Applied Environmental Science, Stockholm University, SE-10691 Stockholm, Sweden.

 doi: 10.1139/F05-172 © 2005 NRC Canada

model of the type of Thomann (1981), where body mass and ^{137}Cs are modeled simultaneously. The radiotracer approach allows estimation of bioenergetic rates that otherwise are extremely difficult or laborious to quantify in the field, e.g., feeding rate (Forseth et al. 1992) or the metabolic costs of activity (Rowan and Rasmussen 1996).

A problem to consider when using ^{137}Cs as a tracer, as well as in radiation monitoring, dose calculations, and model development, is the high variability of radiocesium in freshwater fish. Even at narrow spatial and temporal scales, e.g., within a lake at a single sampling occasion, ^{137}Cs concentrations in fish populations often show a more than twofold variability among similar individuals (Håkanson 1999). Within-lake variation cannot be explained by conservative state variables such as fallout density, salinity, lake trophy, lake morphometry, and watershed characteristics, which are known to cause variability among systems (Håkanson et al. 1992; Sonesten 2001). Also, temporal variability in fish ^{137}Cs, which can be seasonal, interannual, or "stochastic", is typically smaller than the individual variation within systems (see data in Kolehmainen et al. 1967; Elliott et al. 1992; Ugedal et al. 1995). Apart from such external forcing, physiological and ecological processes are likely to contribute to the variance. At steady state, the ^{137}Cs concentration in fish approximately equals the ratio of uptake rate to the sum of the elimination and growth rates (Thomann 1981; Rowan et al. 1998). The uptake rate depends on feeding rate, assimilation efficiency, and ^{137}Cs content in the food. The elimination rate depends on body weight and temperature (Ugedal et al. 1992) and is thus likely metabolically coupled, as is growth rate. These parameters may vary not only among species as such but also among individuals with different activity patterns, habitat, or feeding preferences. At higher levels of organization, the complex balance between bioenergetic and trophic processes may be manifested as significant relationships between fish ^{137}Cs and body size, age, sex, maturity, and diet composition. However, to distinguish and quantify such relationships within natural populations would require large sample sizes because of the compound origin of the typically high variability of ^{137}Cs concentrations among individual fish.

In the present study, we examine a large data set to identify and quantify the sources of variation in ^{137}Cs activity concentrations within and between populations of a freshwater fish community. We test hypotheses about the relationships between the distribution (mean and variance) of ^{137}Cs concentrations and different ecophysiological characteristics of individuals or populations. First, we hypothesize that ^{137}Cs concentrations increase with body size because growth efficiency and elimination rate generally decrease with fish age or weight (Ugedal et al. 1992), whereas assimilation efficiency of ^{137}Cs may increase with size (Kolehmainen 1972). Second, ^{137}Cs concentrations in fish are expected to increase with trophic position if ^{137}Cs undergoes biomagnification, i.e., concentration enrichment along food chains (Rowan and Rasmussen 1994). Third, the ^{137}Cs variance is expected to decrease with increasing population trophic position because random sampling by consumers from the ^{137}Cs distribution of their food organisms would narrow the variance of the consumers relative to that of their prey. Alternatively, if feeding is nonrandom in such a way that trophic position differs among individual fish within populations, the ^{137}Cs variance may increase with trophic position because omnivory potentially increases with each trophic level. Finally, the variance is expected to increase with the population niche width and in particular with functional omnivory, which we define as feeding on food sources with distinctly different ^{137}Cs levels irrespective of prey trophic level. This can be distinguished from the previous hypothesis by examining to what extent food sources at similar trophic levels differ in contamination levels, e.g., ^{137}Cs concentrations of benthic organisms may be elevated owing to interactions with highly contaminated surface sediments (Rowan et al. 1998). In addition to these hypotheses, we evaluate the relationships between fish ^{137}Cs and physiological variables such as body condition, sex, gonadosomatic index (GSI), and the concentrations of water, K, and lipid in muscle tissue.

Our data include radiocesium measurements of more than 1300 fish of seven species caught during 1996–1999 in a Swedish lake. The data cover wide intraspecific size ranges and include information on sex, maturity, and diet of individual fish, variables that rarely are combined in typical monitoring programs. One decade after the Chernobyl fallout, ^{137}Cs levels in affected lakes have approached steady state (Smith et al. 2000). Therefore, our data are unaffected by the highly dynamic situation that can complicate the interpretation of early post-Chernobyl results as shown in earlier data from the same lake (Sundbom et al. 2003).

Methods

Lake Flatsjön (60°29′N, 17°10′E), Sweden, is a humic, mesotrophic, shallow, and polymictic lake (area 0.61 km^2, mean depth 2.5 m) that is usually ice covered from November to mid-April. (see Broberg et al. (1995) for further morphometric and chemical data). The watershed, covered mainly by forest (84%) and peat bogs (7%), received 60–80 kBq·m^{-2} of rain-borne ^{137}Cs during the first days after the Chernobyl accident in 1986 (Broberg et al. 1995). Fish were collected on 18 occasions (March–October) during the period September 1996 – October 1999 using survey gill nets with sections (3 m) of various mesh sizes (10–75 mm). The nets were always placed at the same sites, both along the shore and outwards. Ordered by abundance, the species caught were roach (*Rutilus rutilus*), Eurasian perch (*Perca fluviatilis*), bream (*Abramis brama*), northern pike (*Esox lucius*), ruffe (*Gymnocephalus cernuus*), rudd (*Scardinius erythrophthalmus*), and white bream (*Blicca bjoerkna*).

The fish were frozen shortly after catch and thawed before preparation. Total length, weight, and sex of each fish were determined. In addition, the gonads and gut content of many individuals were weighed separately. When possible, the volumetric proportion of different food organisms in individual guts was visually estimated. The gut content was sorted into four diet classes: plants, benthic invertebrates, zooplankton, and fish. The relative gut fullness was measured at a four-level scale: empty, almost empty, half full, and full. Potassium and lipid concentrations in muscle tissue were determined for 42 perch of similar size. Potassium was measured by flame emission spectroscopy after nitric acid digestion.

© 2005 NRC Canada

Lipid content was determined by weighing a lyophilized sample before and after chloroform extraction.

Muscle tissue and, for some fish, gonads were put into scintillation vials, lyophilized, and compacted before radiometric analysis. Most samples contained tissue from single individuals, but occasionally, samples from several similarly sized individuals were mixed in the same vial. Both the fresh and dry weights (fw and dw, respectively) of the samples were recorded. Activity concentrations of ^{137}Cs were quantified using a gamma counting system (Intertechnique model 4000) equipped with a NaI well detector. The equipment was regularly calibrated using blanks and dry standards of highly contaminated lichens collected early after the Chernobyl fallout. All measurements were corrected for background radiation and sample geometry. Corrections for ^{134}Cs and ^{40}K were not necessary, since interference from these nuclides proved to be negligible. Counting times were adjusted to obtain a standard error below 1%. For samples with low activity (<1.7 Bq), the counting error exceeded this limit, but it was always below 3%.

Calculations

Because perch typically undergo ontogenetic diet shifts, we divided perch into four size classes based on diet. The average diet composition as a function of body length was estimated using a multicategory logistic regression model (Agresti 1996, pp. 205–209; SAS Institute Inc. 2000) with three diet categories: zooplankton, zoobenthos, and fish. Perch shorter than 9.8 cm were mainly zooplanktivorous (perchZ), 9.8- to 15.1-cm perch fed mainly on zoobenthos (perchB), 15.1- to 24-cm perch had a mixed diet of zoobenthos and fish (perchBF), and perch above 24 cm were mainly piscivorous (perchF).

Activity concentrations were corrected for radioactive decay back to 1 May 1986 and log transformed to equalize variance among fish types (species or perch size class). Original data were used for comparisons within a fish type because log transformation generally did not improve normality (Table 1). In statistical tests and estimation of least-squares means and moments, calculations were weighted by the number of fish in each sample to account for the assumed smaller variance of pooled samples. Further, activity concentrations were corrected for differences in ^{137}Cs concentration between sampling dates. This was done by dividing individual ^{137}Cs concentrations with the least-squares mean of each date and fish type and multiplying by the overall mean of each fish type. The least-squares means were estimated with analysis of covariance (ANCOVA) with body length as linear covariate taking into account that the size of analyzed fish may have differed among sampling dates. This method is preferable to using arithmetic or geometric means for the temporal correction if data are size dependent. Activity concentrations refer to muscle tissue (fw) unless noted otherwise. JMP software (SAS Institute Inc. 2000) was used in all statistical analyses.

The water content was calculated from the mass lost after lyophilization of tissue samples. Condition factors (CF) were calculated according to Le Cren (1951) as

$$CF = \frac{W}{aL^b}$$

Table 1. Descriptive statistics of ^{137}Cs activity concentrations (Bq·kg^{-1} fresh weight) of fish populations in Lake Flatsjön.

	n_{fish}	$n_{samples}$	Range	Interquartile range	CV (%)			Mean				P_r normal	P_r lognormal
					Linear	Geometric	Median	Mean	geometric	Skewness	Kurtosis		
All fish	1361	1192	376–8241	944–2664	78	49	1397	1862	1502	1.44	1.17	<0.001	<0.001
Roach	509	390	438–1691	848–1084	21	19	960	970	955	0.42	0.28	0.030	0.170
Bream	94	83	535–1170	757–918	17	16	853	824	827	0.11	–0.55	0.726	0.134
Northern pike	93	93	1117–5378	2322–2969	24	22	2693	2731	2654	0.97	2.53	0.002	0.334
Rudd	29	29	376–2861	460–854	69	39	614	782	675	2.75	8.98	<0.001	0.010
Ruffe	30	27	697–2440	947–1344	35	26	1206	1206	1158	1.73	3.45	<0.001	0.114
White bream	19	17	387–941	510–867	26	25	725	696	669	–0.32	–1.45	0.208	0.119
Perch (all)	387	353	508–8241	1612–4058	55	42	2117	2789	2429	0.81	–0.34	<0.001	<0.001
PerchZ	129	109	1053–2456	1486–1870	20	19	1681	1730	1652	0.27	–0.58	0.641	0.199
PerchB	167	153	508–2831	1369–1805	23	22	1580	1580	1541	0.17	0.38	0.969	0.013
PerchBF	196	196	907–6413	2770–4235	32	33	3596	3451	3229	–0.30	–0.32	0.008	<0.001
PerchF	95	95	3154–8241	4255–5592	20	17	4699	4984	4893	1.00	0.83	<0.001	0.071

Note: The P_r values correspond to the Shapiro and Wilk's W for testing whether the ^{137}Cs levels deviate from normal or lognormal distributions.

© 2005 NRC Canada

Table 2. (*a*, *b*) Contribution of time and body size to the total variation of ^{137}Cs activity concentrations within fish populations in Lake Flatsjön. R^2 was estimated by ANOVA and ANCOVA with sampling occasion as a nominal variable and length as covariate. (*c*) Size- and time-independent measures of individual variation: root mean square error (RMSE), CV, and the relative quantile deviation, $(p_{90} - p_{10})/(2p_{50})$, of the residuals of ANCOVA. (*d*) Probabilities corresponding to Shapiro and Wilk's *W* for testing whether the residuals of ANCOVA deviate from normal or lognormal distribution. (*e*) Mean diet composition estimated from individual gut contents. (*f*) Various trophic indices: biomagnification factor (BMF), trophic position of each population, Levins' index of niche width, and functional omnivory index.

Fish type	Roach	Bream	Northern pike	PerchZ	PerchB	PerchBF	PerchF
(*a*) ANOVA							
R^2	0.11	0.24	0.27	0.55	0.43	0.21	0.39
n	390	83	93	109	153	196	95
p, sampling date	<0.001	0.083	0.022	<0.001	<0.001	<0.001	<0.001
(*b*) ANCOVA							
R^2 (*n* as in ANOVA)	0.44	0.51	0.46	0.59	0.43	0.30	0.53
p, date	<0.001	0.073	0.011	<0.001	<0.001	0.001	<0.001
p, length	<0.001	<0.001	<0.001	0.004	0.951	<0.001	<0.001
(*c*) Residual dispersion							
RMSE (Bq·kg^{-1} fresh weight)	147	95	489	221	274	936	687
CV linear	0.15	0.11	0.18	0.13	0.17	0.27	0.14
CV geometric upper	0.17	0.12	0.18	0.14	0.21	0.40	0.14
$(p_{90} - p_{10})/(2p_{50})$	0.17	0.13	0.25	0.16	0.20	0.36	0.19
(*d*) Residual distributions							
p, normal	0.002	0.117	<0.001	0.105	0.479	0.005	0.910
p, lognormal	0.002	0.434	0.067	0.002	0.576	<0.001	0.930
(*e*) Diet composition (%)							
Plants	52	36	0	0	0	0	1
Zoobenthos	40	59	13	24	63	56	24
Zooplankton	7	5	0	76	37	0	0
Fish	0	0	87	0	0	43	75
(*f*) Trophic indices							
BMF	4.6	4.0	2.4	4.0	5.8	5.2	4.6
Trophic position	2.5	2.6	3.6	3.0	3.0	3.3	3.5
Levins' index	2.3	2.1	1.3	1.6	1.9	2.0	1.6
Functional omnivory	0.35	0.30	0.75	0.52	0.59	1.11	0.97

where W is fish weight, L is total length, and a and b are the intercept and slope of the length–weight relationship of each species ($\ln W = \ln a + b \ln L$). This formulation centers the CF on unity and enables comparisons among fish of different species and size. Where adequate, the CF was based on somatic weights after subtraction of gonad mass.

The average trophic position (TP) of the different fish types was calculated using the formula employed by Vander Zanden and Rasmussen (1996):

$$\mathrm{TP} = \sum P_i D_i + 1$$

where P_i is the proportion of the ith diet type and D_i is the trophic level of the ith diet type. Mean P of each fish type was estimated from the gut content of individual fish (Table 2*e*). Plants were assigned to trophic level 1, zoobenthos and zooplankton were assumed to represent trophic level 2, and prey fish represented trophic level 3. The dietary niche width of each fish type was calculated according to Levins (1968) as $(\sum P_i^2)^{-1}$.

Levins' index becomes 1 for equal diet and increases with food diversity. As a measure of the diversity of ^{137}Cs levels in the food of each fish type, we used the mean squares of the relative difference in ^{137}Cs concentration of each diet class and the average diet weighted by the proportion of each diet class:

$$\sum P_i \left(\ln C_i - \sum \frac{P_i \ln C_i}{n} \right)^2$$

where C_i is the ^{137}Cs activity concentration of the ith diet class and n is the number of diet classes. We denote this index the functional omnivory index. It is functional with regard to ^{137}Cs and increases, from zero at uniform food ^{137}Cs, with the divergence in ^{137}Cs concentrations between food categories. Thus, omnivory here refers to the utilization of food sources that differ in ^{137}Cs concentration rather than the traditional definition of omnivory as the feeding from more than one trophic level. ^{137}Cs activity concentrations (Bq·g^{-1} dw) of the diet classes during 1996–1999 in Lake Flatsjön were 0.55 ± 0.06 (mean ± SE, n = 5) in mixed littoral zoobenthos, 1.87 ± 0.18 (n = 8) in zooplankton (>200 µm), and 0.85 ± 0.25 (n = 11) in submerged macrophytes (M. Sundbom, unpublished data). For fish diet, we used data on small perch and roach (<12 cm) from the present study. The average ^{137}Cs in these fish was 6.87 Bq·g^{-1} dw.

© 2005 NRC Canada

These concentrations were weighted by the percentages of the different diet categories to estimate the typical ^{137}Cs concentration in the diet of each fish type. The biomagnification factor (BMF) was then calculated by dividing the average ^{137}Cs concentration (Bq·g^{-1} dw) of each fish type by the estimated average ^{137}Cs concentration of their food. Prey contamination was based on whole organisms. BMFs were therefore corrected for the relative difference in ^{137}Cs concentration between muscle tissue and whole fish. Data on the ^{137}Cs concentration (Bq·g^{-1} fw) in muscle relative to that in whole fish were obtained from Saxén et al. (2002) and averaged at 1.31 (roach), 1.45 (bream), 1.25 (pike), and 1.32 (perch).

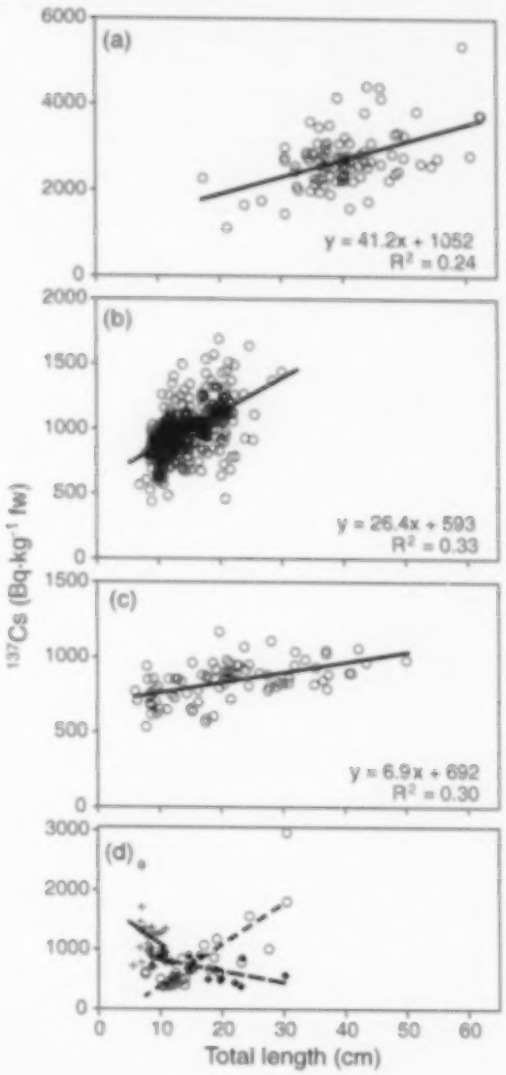
Results

Activity concentrations of ^{137}Cs (hereafter referred to as just ^{137}Cs) in the whole fish community had a highly skewed distribution, with an overall mean of 1862 Bq·kg^{-1} fw and a coefficient of variation (CV) of 72% (Table 1). For the most contaminated individuals, ^{137}Cs was 22 times higher than for the least contaminated individuals. Although much of this variation resulted from differences between species, there was a considerable intraspecific variation with CVs ranging from 17% for bream to 69% for rudd (Table 1). The frequency distributions of ^{137}Cs were positively skewed except for white bream and perchBF. No generalizations could be made about kurtosis or the type of distribution. In some fish types, ^{137}Cs successfully fitted the normal or the lognormal distribution whereas in other the data differed significantly from both (Table 1; Figs. 1 and 2*a*). For example, ^{137}Cs in perch had a bimodal distribution (Fig. 2). Because ^{137}Cs varied with body size in most fish types (see below), the distributions can be biased by population structure or inadvertent sampling selectivity. In addition, temporal variability may bias the distributions if ^{137}Cs in fish were extremely low or high during certain periods. To find the typical distribution of ^{137}Cs, we reanalyzed data after accounting for fish size and sampling time. However, the type of distribution varied among fish types in a nonconsistent manner also for these normalized data (Table 2*d*).

Temporal variability

Over the 3-year sampling period, there was no significant long-term trend in ^{137}Cs in any species of fish (Fig. 3). However, there were significant differences among sampling occasions owing to seasonal or stochastic variability, which accounted for 7% of the total variance in log ^{137}Cs (analysis of variance (ANOVA), $F_{[17,1174]} = 5.27$, $R^2 = 0.071$, $p < 0.0001$). When analyzing each species separately, the temporal variation was significant in perch ($R^2 = 0.12$, $p < 0.0001$), pike, and roach (Table 2*a*) but not in bream, rudd, ruffe, and white bream. Total individual variation substantially exceeded any temporal variation in ^{137}Cs (Fig. 3). The temporal variation of mean ^{137}Cs levels, expressed as the ratio of maximum/minimum among occasions, was 1.3-fold for the whole community and 1.3- to 2-fold for different subpopulations at sample sizes of $n \geq 10$.

Fig. 1. Activity concentrations of ^{137}Cs and body length of (*a*) northern pike (*Esox lucius*), (*b*) roach (*Rutilus rutilus*), (*c*) bream (*Abramis brama*), and (*d*) ruffe (*Gymnocephalus cernuus*) (+, solid line), rudd (*Scardinius erythrophthalmus*) (○, short-dashed line), and white bream (*Blicca bjoerkna*) (◆, long-dashed line) in Lake Flatsjön.

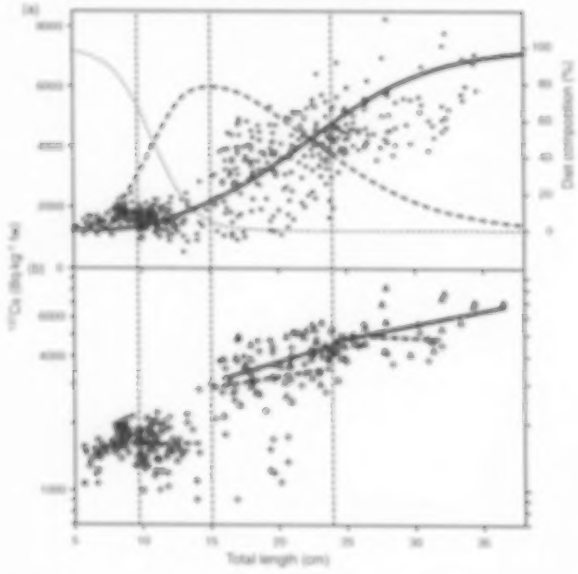


Size relationships

Activity concentrations increased with fish size in all species except for ruffe and white bream (Figs. 1 and 2). The steep increase in ^{137}Cs with size in rudd resulted from a few large individuals with exceptionally high levels. White bream, ruffe, and rudd were caught in low numbers and are therefore not analyzed in further detail. For the main populations, size alone irrespective of species accounted for 27% of the variance (Table 3). ^{137}Cs increased linearly with fish length in roach, bream, and pike (Fig. 1), although the concentrations in bream appeared to level off at a length of

© 2005 NRC Canada

Fig. 2. (*a*) Stepwise increase of ^{137}Cs activity concentrations with body length in Eurasian perch (*Perca fluviatilis*) in Lake Flatsjön. The vertical broken lines separate the four size classes perchZ, perchB, perchBF, and perchF (from left to right). The sigmoid curves were estimated by logistic regression and show the proportion of different food categories as a function of body length (short-dashed line, zooplankton; long-dashed line, zoobenthos; solid line, fish). (*b*) A subset of the data in Fig. 2*a* on a logarithmic scale including only individuals with known diet. Different symbols indicate the predominant diet category found in individual stomachs: zooplankton (○), zoobenthos (+), or fish (△). Straight lines represent the ^{137}Cs–length relationship within size classes for fish with different diet.

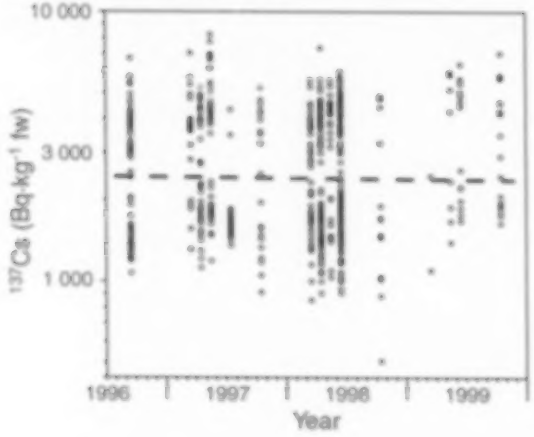


about 20 cm. Residual inspection suggests that the variance was independent of length in pike, roach, and bream. In contrast, perch displayed a stepwise increase in ^{137}Cs with length by in total about sixfold, and the variance was higher in the two larger size classes, especially in perchBF (Fig. 2*a*). Also within perch size classes, ^{137}Cs increased significantly with length except for perchB (Table 2*b*). There was a positive ^{137}Cs–size relationship across species but less clear than within species (Fig. 4). The positive trend was due to piscivores being generally larger and more contaminated. If treating nonpiscivorous fish separately, ^{137}Cs actually decreased with the geometric population mean of body weight (R^2 = 0.79, p = 0.007) (Fig. 4). Sampling date and body length together accounted for 30%–59% of the individual ^{137}Cs variation of the different fish types (Table 2*b*), implying that 41%–70% of the variance must be generated by other factors.

Ecophysiological traits

The effect of different ecophysiological factors on time-corrected and log-transformed ^{137}Cs levels was investigated using a series of linear models, including body length as covariate (Table 3). Independent variables that were correlated with length were regressed against the residuals of a

Fig. 3. Activity concentrations of ^{137}Cs in muscle tissue of Eurasian perch (*Perca fluviatilis*) during 1996–1999 in Swedish Lake Flatsjön demonstrating greater variability among individuals than over time. The slope of the broken line was calculated by linear regression (log ^{137}Cs versus time) and corresponds to an ecological half-life of 108 years. The slope does not significantly differ from zero (p = 0.82, n = 553). Given the high individual variability, a longer time series would be required for reliable determination of the ecological half-life.



simpler model rather than included in a more complex one to minimize spurious intercorrelation effects. Fish species alone accounted for 64% of the variance, and 89% if combined with size (Table 3). Substituting perch for its four size classes improved the model fit to 88%, even without considering fish size (Table 3). The difference in ^{137}Cs concentration among fish types was statistically significant, as were all pairwise comparisons (Tukey–Kramer honestly significant difference, $Q_{[7,1111]}$ = 2.95, α = 0.05). Piscivorous fish types had higher mean levels than other fish: ^{137}Cs was about three times higher in pike and perch than in the cyprinids and ruffe. ^{137}Cs generally increased with body length, and the interaction between fish type and length was statistically significant. The latter term takes into account that the ^{137}Cs–length slope may differ among fish types. Fish type, length, and their interaction accounted for 91% of the total variation. Additional factors only marginally improved R^2, although their effects were often highly significant. There was no significant difference in ^{137}Cs between males and females if accounting for body size. Radiocesium decreased with the GSI, but the decrease was significant only for female perch (Table 3). Further, ^{137}Cs decreased with the CF, which was positively correlated with the GSI. However, ^{137}Cs also decreased significantly with CF based on somatic length–weight relationships where the gonads had been subtracted from the total body weight (Table 3). There was a small but significant increase in ^{137}Cs (based on dry weight to reduce potentially spurious correlations) with the water content of muscle tissue (Table 3). The negative relationship with CF was significant for all fish types but pike, and the positive relationship with water content was significant for all fish types but perchBF. There was no relationship be-

© 2005 NRC Canada

Table 3. Summary of statistical tests of the relationships between ^{137}Cs levels in fish (Bq·kg^{-1} fresh weight) and different ecophysiological factors.

	Dependent variable	Independent variables (df)	R^2 adjusted stepwise	RMSE stepwise	n stepwise	F	p
Total variation	log ^{137}Cs	None	—	0.284	1112	—	—
Model 1*a*, regression	log ^{137}Cs	*L* (1)	0.270	0.242	1112	412	<0.0001
Model 1*b*, ANOVA	log ^{137}Cs	Species (3)	0.643	0.170	1112	665	<0.0001
Model 1*c*, ANCOVA	log ^{137}Cs	Species (3)	0.643	0.170	1112	1538	<0.0001
		L (1)	0.833	0.116	1112	627	<0.0001
		Species × *L* (3)	0.889	0.095	1112	187	<0.0001
Model 2, ANCOVA	log ^{137}Cs	FT (6)	0.880	0.0982	1112	437	<0.0001
		L (1)	0.900	0.0897	1112	48.7	<0.0001
		FT × *L* (6)	0.906	0.0869	1112	13.1	<0.0001
Model 3, ANCOVA	log ^{137}Cs	FT (6)	0.880	0.0982	1112	467	<0.0001
		L (1)	0.900	0.0897	1112	6.8	0.0092
		FT × *L* (6)	0.906	0.0869	1112	7.8	<0.0001
		Sex (1)	0.893	0.0903	908	2.8	0.0936
Model 4, ANCOVA	log ^{137}Cs (Bq·kg^{-1} dw)	FT (6)	0.871	0.101	1068	419	<0.0001
		L (1)	0.890	0.0930	1068	42.3	<0.0001
		FT × *L* (6)	0.896	0.0905	1068	12.0	<0.0001
		CF (1)	0.899	0.0886	1050	53.2	<0.0001
		WC (1)	0.906	0.0858	1028	56.0	<0.0001
Model 5, AVOVA	Residuals model 2	GF (3)	0.003	0.0858	745	1.8	0.147
Model 6, ANOVA	Residuals model 2	Individual diet (3)	0.031	0.0883	442	5.7	0.0008
Model 7, regression	Residuals model 3	GSI (1)	0.012	0.0884	578	12.9	0.0004
		CFg (1)	0.035	0.0874	578	15.1	0.0001
		GSI × CFg (1)	0.035	0.0873	578	1.4	0.2423

Note: Data were corrected for temporal variability before analysis. Independent variables were added stepwise in the multivariate models. The F statistics and p values for each variable refer to the final model. FT, fish type (seven classes); *L*, body length (cm); CF, condition factor; WC, water content (% fw); GF, gut fullness; GSI, gonadosomatic index (% fw); CFg, condition factor excluding gonad mass; RMSE, root mean square error.

tween the relative gut fullness and ^{137}Cs (Table 3). Potassium and lipid concentrations of muscle tissue were measured in 42 perch of similar size (16–20 cm) but with a wide contamination range (1100–5000 Bq·kg^{-1} fw). Concentration ranges of K and lipid were 12–16 ppm and 5%–15% (dw/dw), respectively. However, there was no relationship between ^{137}Cs and concentrations of K ($p = 0.54$) or lipids ($p = 0.97$).

Diet and ^{137}Cs

The BMF based on the ratio of the mean whole-body ^{137}Cs in fish to ^{137}Cs in the average diet (dw/dw) ranged from 2.4 in pike to 5.8 in perchB (Table 2*f*). The mean BMF based on the regression slope between log ^{137}Cs of fish and the mean trophic position (Table 2*f*) was 3.9 ($R^2 = 0.84$, $p = 0.004$). Dietary differences, especially with respect to prey trophic level, may thus explain much of the variation in ^{137}Cs among fish types.

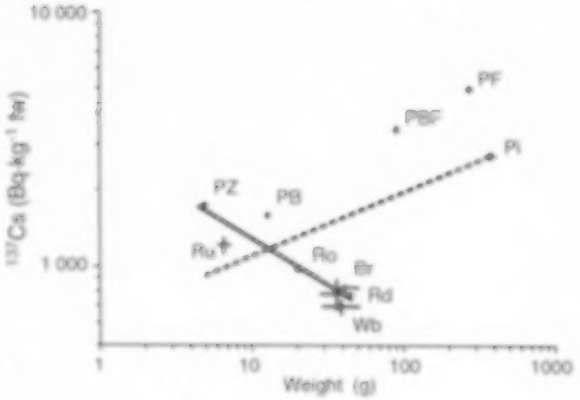
Dietary differences also influenced the ^{137}Cs variation within populations: the ^{137}Cs concentration (after accounting for fish type and size) differed significantly among individual fish with different diet based on the predominant diet category (plants, zoobenthos, zooplankton, or fish) found in their guts (Table 3). The population least-squares means of ^{137}Cs ranked in the same order as ^{137}Cs in the diet classes: fish, zooplankton, plants, and zoobenthos. Post hoc tests show that individuals with fish in the gut had significantly higher ^{137}Cs levels than other fish ($F_{[1,438]} = 7.6$, $p = 0.006$). In addition, fish with plants or zooplankton in the gut had higher levels than fish that had fed on zoobenthos ($F_{[1,438]} = 5.7$, $p = 0.017$). The ^{137}Cs levels in piscivorous individuals averaged 10% higher than those of benthivores and 5% higher than those of herbivores and zooplanktivores. Note that the use of the terms piscivore, etc., does not imply here that individual fish were dedicated to a single food source. The terminology refers merely to the composition their last meal. Among the perchBF with extremely low ^{137}Cs concentration, all gut-analyzed individuals had fed on benthos, and among the perchF with extremely high ^{137}Cs concentration, all had fed on fish shortly before they were caught (Fig. 2*b*). The difference in ^{137}Cs between benthivorous and piscivorous perchBF was significant (Wilcoxon rank sum test, $p < 0.01$). There was a tendency of a similar pattern in perchF, and ^{137}Cs levels in benthivorous perch*Z* and perchB were on average lower than in zooplanktivores (Fig. 2*b*). Furthermore, pike that had fed on perch had higher ^{137}Cs levels than pike with roach or unidentified fish in the stomach (*t* test, $p < 0.05$), which is consistent with the observed difference in ^{137}Cs between the two prey fish. The observed relationships between ^{137}Cs and diet indicate that feeding histories among individual fish differ within populations.

Variance patterns

The relationships between the time- and size-independent component of the ^{137}Cs variance and various feeding indices on the population level were investigated by using the residual dispersion of the model in Table 2*b*. We investigated the

© 2005 NRC Canada

Fig. 4. ^{137}Cs activity concentrations and body weight of different fish populations in Lake Flatsjön (geometric mean ± SE). Lines represent log–log regressions including all fish types (broken line) or nonpiscivorous fish only (solid line). Br, bream (*Abramis brama*); Pi, northern pike (*Esox lucius*); PB, perchB; PBF, perchBF; PF, perchF; PZ, perchZ (*Perca fluviatilis*); Rd, rudd (*Scardinius erythrophthalmus*); Ro, roach (*Rutilus rutilus*); Ru, ruffe (*Gymnocephalus cernuus*); Wb, white bream (*Blicca bjoerkna*).



relationships at both absolute and relative scales of ^{137}Cs variability by using either the root mean square error (RMSE) or the relative quantile deviation expressed as the semirange between the 10th and 90th percentiles of the residuals relative to the median (Table 2*c*). The latter is independent of outliers and better suited for comparisons of distributions that are highly skewed in different directions than are parametric measures of relative variability, such as the CV and the standard deviation of logarithms. The residual variance of ^{137}Cs differed significantly among the fish types (Bartlett's test for homogeneity of variance, $p < 0.0001$). Levins' niche index ranged from 1.3 in almost exclusively piscivorous pike and zooplanktivorous perchZ to 2.3 in roach (Table 2*f*), but niche width was not correlated with ^{137}Cs residual variation (Fig. 5). There was a positive correlation between residual variation and fish trophic position (Fig. 5), but only on the absolute variability scale. The relationship between the residual variation and functional omnivory was significant on both absolute and relative scales, and the positive correlation was better than for trophic level (Fig. 5). Functional omnivory appeared to be correlated also with the CV but this was not significant ($R^2 = 0.50$, $p = 0.077$). The correlation and degree of significance were generally better on absolute than relative scales of variability. This difference was largely caused by the comparatively low variability despite a high contamination level in perchF and vice versa in perchBF.

Discussion

Magnitude and distribution of ^{137}Cs variation

The variation of ^{137}Cs activity concentrations was substantial both within and among the seven fish species of Lake Flatsjön. The intraspecific CVs obtained here (range 0.17–0.55, mean 0.35, median 0.26) are comparable with a recent compilation of post-Chernobyl data reporting CVs of up to 1.4 with a mean of 0.22 (Håkanson 1999), which suggests that a high within-species variation in ^{137}Cs is common in freshwater fish. Based on the individual variation observed here, the sample size required for obtaining a sample mean within 10% on either side of the true mean is 22 for small perch (perchZ + perchB) and 44 for large perch (perchBF + perchF). These numbers were iteratively calculated according to Zar (1999).

Oleksyk et al. (2002) hypothesized that ^{137}Cs levels in fish are normally, or at least more symmetrically, distributed than in terrestrial animals. Another hypothesis states that biotic concentrations of nonessential trace elements, such as Cs, are lognormally distributed (Liebscher and Smith 1968; Pinder and Giesy 1981). Although the distributions of ^{137}Cs in fish often were positively skewed in Lake Flatsjön, the present study fails to clearly support these hypotheses. Any uniformity in distributions among fish types or distribution changes with, e.g., fish trophic position could not be found, despite a large data set. Formal tests for differentiating among standard frequency distributions obviously require massive amounts of data.

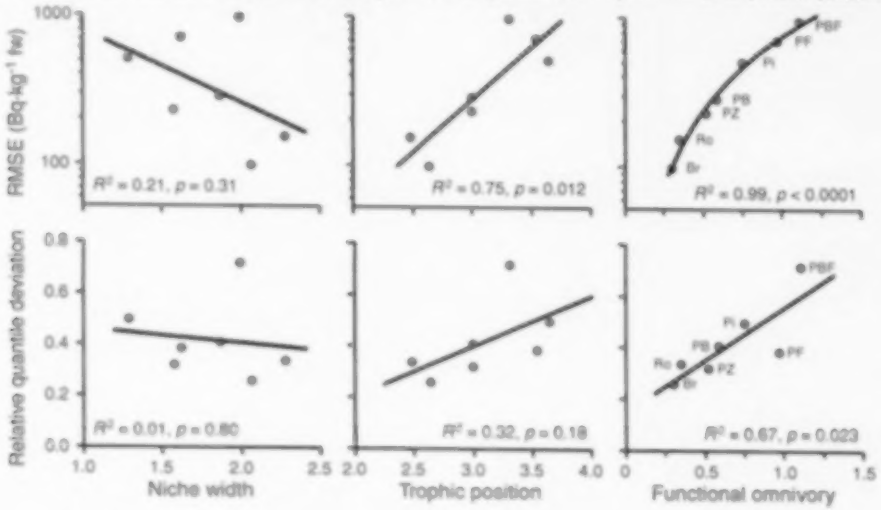
Ecophysiology and ^{137}Cs variation

Our evaluation identified a number of biotic factors of importance for both the mean levels and the variability of ^{137}Cs in fish. In accordance with previous studies (Sundbom et al. 2003 and references therein), ^{137}Cs increased with body size in most species. The slopes differed among species, which may reflect differences in the ontogenetic development of bioenergetics and feeding ecology (Ugedal et al. 1995; Rowan et al. 1998). For example, the match of the stepwise increase in ^{137}Cs with the transition to piscivory in perch suggests that feeding ecology amplifies the size effect in this species. In addition to interspecific differences, the ^{137}Cs–size relationship can show variation among lakes (Sonesten 2001). There is apparently no simple and general method to generate adequately size-corrected data for ^{137}Cs in fish. This is further illustrated by the lack of a consistent size effect across species. It is possible that a more consistent ^{137}Cs–size relationship and some additional explanation of the total variance can be obtained by including age. In the present study, we have used fish size rather than age as a covariate, mainly because size data are routinely available and contain less analytical bias than age data. However, the quantitative importance of age effects on bioaccumulation, beyond those associated with size, is poorly known and should be further explored, for example by cross-system field studies considering also fish age in addition to fish size.

About half of the within-population variation was here accounted for by time- and size-independent factors. Thus, the variability among apparently similar individuals is not random but can at least to some extent be explained with additional effort. Radiocesium in fish decreased with the CF. Similar patterns have been observed within systems for ^{137}Cs in largemouth bass (*Micropterus salmoides*) (Whicker et al. 1997) and Hg in yellow perch (*Perca flavescens*) (Greenfield et al. 2001) at presumably nontoxic contamination levels. The negative relationship between ^{137}Cs and body condition may be caused by growth dilution because increased body condition can be associated with periods of

© 2005 NRC Canada

Fig. 5. Relationship between time- and size-independent variation of ^{137}Cs activity concentrations and the niche width, trophic level, and functional omnivory in different fish types. The given measures of variability are the standard deviation (root mean square error) and the relative quantile deviation, $(p_{90} - p_{10})/(2p_{50})$, of the residuals from the model in Table 2*b*. Br, bream (*Abramis brama*); Pi, northern pike (*Esox lucius*); PB, perchB; PBF, perchBF; PF, perchF; PZ, perchZ (*Perca fluviatilis*); Ro, roach (*Rutilus rutilus*).



high growth rates. Ugedal et al. (1995) found a negative correlation of ^{137}Cs with growth rate and accordingly a positive correlation with body size. However, after correcting for the size effect, growth dilution may be difficult to detect by simply comparing contaminant concentrations with growth rates. This is because the temporal resolution of growth rate measurements usually is low, and over longer time periods, growth and feeding rates are correlated, which may mask any effect of growth dilution.

Females had higher ^{137}Cs levels than males on average. After correcting for size, however, males tended to have higher levels than females, as earlier observed by Holloman et al. (1997). Yet in other studies, the effect of sex on ^{137}Cs in fish was undetectable (Kulikov and Kulikova 1977; McCreedy et al. 1997) or variable (Newman and Brisbin 1990). Rowan et al. (1998) found a stepwise increase in biomagnification during maturation in some species but not in others. They attributed the difference to a combination of species-specific changes in metabolism during maturation and spawning losses of ^{137}Cs caused by different GSI or gonad ^{137}Cs content. In the present study, the mean GSI was higher in female perch (mean = 16%) than in female roach (9.6%), whereas the GSI of males was equally low in both species (3%). The ^{137}Cs concentration in gonads relative to that in muscle was also higher in female perch (69%) than in roach (45%). Multiplication suggests a 2.6-fold higher loss of ^{137}Cs at spawning in perch than in roach, which may explain the negative relationship between ^{137}Cs (in muscle) and GSI observed in female perch but not in roach or male perch. Note, however, that the stepwise increase in perch ^{137}Cs with body size coincided with the transition to piscivory (≈16 cm length) rather than with maturation (males = 8 cm, females = 12 cm).

Individual variations in ^{137}Cs elimination rates and assimilation efficiency are potentially important sources of variation in ^{137}Cs concentration among fish. Feeding and growth rates are probably of less importance, as these rates are positively correlated and have opposite effects on bioaccumulation. Only a few published studies provide estimates on the variability in elimination rate and assimilation efficiency of ^{137}Cs. Ugedal et al. (1992) obtained high R^2 (median = 0.98) and low CVs (median = 7%) when estimating the elimination rate of ^{134}Cs within size classes of brown trout (*Salmo trutta*) in the laboratory. In a related study, Forseth et al. (1992) found that percent assimilation varied among prey types. Within prey treatments, however, the standard errors were low (1%–5%, n = 10). Similarly, low individual variability was recently found for experimentally determined assimilation efficiencies of alkali metals (Cs, Rb, and K) in Atlantic salmon (*Salmo salar*) (Kennedy et al. 2004). These studies suggest low intraspecific variability among fish of similar size, which may explain the low variability ^{137}Cs in a school of 39 small perch from Lake Flatsjön (not included in the main data set because only the dry weights of samples were available). These fish were caught on the same day within about 1 m^2 of the net, all heading in the same direction. The fish were of similar size (10.2–10.8 cm) and had probably very small dietary differences, since the catch conditions indicated that they were shoaling and foraging together. The CV of ^{137}Cs (becquerels per gram dry weight) was only 5% (including a gamma-counting error of 1%–2%), whereas for all similar-sized perch, the overall CV was 20% even after time correction. The increase in variability with decreasing "similarity" of catch conditions suggests that variability of ^{137}Cs in the food was as important, if not more, for the observed residual variability of ^{137}Cs among fish as was individual variability in bioenergetics or assimilation efficiency.

Biomagnification and its variation

Piscivorous fish types had higher mean ^{137}Cs levels than all other fish types. The average ± SE BMF based on ^{137}Cs

© 2005 NRC Canada

in the diet was 4.36 ± 0.40, which is similar to the mean of 3.80 ± 0.17 reported by Rowan et al. (1998). The direct estimate also agrees with the regression-based factor of 3.9 that was estimated from the ^{137}Cs – trophic position relationship, which in turn is a little higher than the two- to three-fold increase in ^{137}Cs per trophic level found in a regression-based evaluation of a global data set (Rowan and Rasmussen 1994). Our evaluation provides further support of biomagnification of Cs and suggests a typical BMF of around 4 in freshwater fish.

Carnivorous Odonata larvae were a common prey of perchB, whereas filter-feeding crustaceans dominated the diet of perchZ. If biomagnification exists within invertebrate food webs, we would have expected higher ^{137}Cs levels in benthivores than in planktivores, as found by Rowan et al. (1998). However, we found higher levels in perchZ than in perchB, and benthivorous individuals had on average the lowest ^{137}Cs concentrations, which is consistent with the threefold higher ^{137}Cs concentration of zooplankton than of zoobenthos (see Methods). This may also explain the negative relationship between ^{137}Cs and size across nonpiscivorous fish types, since pelagic feeders in Lake Flatsjön were typically small (young roach and perchZ), whereas littoral feeders were often large (bream and rudd). A lower assimilation efficiency of ^{137}Cs in fish feeding on benthic insects than in fish feeding on zooplankton (Forseth et al. 1992) may also have contributed to the observed difference between pelagic and littoral feeders. A higher sensitivity of fish to contamination via the pelagic than via the benthic food web has been reported for other contaminants, such as chlorinated organics (Kidd et al. 2001) and Hg (Power et al. 2002). The apparent lack of biomagnification in invertebrates may be explained by direct uptake of ^{137}Cs being relatively more important than trophic uptake in small aquatic organisms. Our results disagree with the assumption that benthic invertebrates and benthivores accumulate more ^{137}Cs than zooplankton and planktivores if in close association with large inventories of ^{137}Cs in the sediments (Rowan et al. 1998). Even in highly organic sediments, as in Lake Flatsjön, ^{137}Cs is largely controlled by strong sorption to clay particles (cf. Wauters et al. 1996). Further, more than 10 years after fallout, ^{137}Cs levels in sediments have reached steady state with respect to ^{137}Cs in the open water (Smith et al. 2000). Ingestion of sediment is thus not expected to have significantly influenced bioaccumulation of ^{137}Cs in the present study. On the other hand, the sorption kinetics of Cs to clays are known to be slow and complex, which may result in temporal shifts in the apparent equilibrium between sediments and overlying water and thus contribute to the difficulties in predicting the sediment influence on bioaccumulation in benthivores. Contamination may either increase by ingestion of sediment if clay-bound ^{137}Cs is readily bioavailable or decrease if ingested clay adsorbs the ^{137}Cs released from food organisms during digestion. In the present study, however, invoking the hypothesis of sediment influence (or differential assimilation among prey) is not needed to explain the differences in ^{137}Cs among the trophic groups of fish, since differences in food ^{137}Cs alone appear to be sufficient.

Trophic position accounted for 85% of the ^{137}Cs variation among fish types in this study. The residual variation may be due to differences in biomagnification, for example as a result of interspecific differences in metabolic rate (Rowan et al. 1998) or assimilation efficiency. Perch of all size classes were more contaminated than other species with comparable trophic positions, which has been noted in other recent studies as well (Sundbom et al. 2003 and references therein). Percids may generally be more susceptible to radiocesium bioaccumulation than other fish. In the present study, the benthivorous ruffe had higher ^{137}Cs levels than the cyprinid benthivores, and in another study, the piscivorous yellow perch and walleye (*Sander vitreus*) had higher levels than pike (Rowan and Rasmussen 1996). High feeding rate owing to higher metabolism in perch than in roach has been suggested as an explanation, at least shortly after a pulse contamination (Meili 1991). On the other hand, the feeding rate and metabolic cost of activity of yellow perch and walleye, based on bioenergetic modeling of ^{137}Cs at steady state, were among the lowest of the 14 species studies in Ottawa River (Rowan and Rasmussen 1996). Other possible explanations of the generally higher ^{137}Cs levels in percids include a longer biological half-life of ^{137}Cs in perch compared with that in roach over a wide body size range (Häsänen et al. 1967) and high assimilation efficiency either resulting from the slow gut evacuation rate of perch (Elliott et al. 1992) or related to lower gut pH in percids than in cyprinids (Western and Jennings 1970; Hadderingh et al. 1997). The perch has a distinctly detached stomach, and the hypothesis of high assimilation efficiency in perch is credible. However, a specific study is required to clearly identify the mechanisms behind the generally elevated levels of ^{137}Cs in perch.

Effect of individual resource specialization

After accounting for sampling time and fish type and size, the ^{137}Cs variation among individual fish still remained substantial. Although we found significant relationships between ^{137}Cs and several physiological factors, these accounted for little of the residual variation. In previous studies, this usually large and apparently unexplained variation was suggested to result from variable feeding habits among individuals (Elliott et al. 1992; Ugedal et al. 1995; Holloman et al. 1997). The major pathway of radiocesium to fish is via the food and the biological half-life ranges from months to years depending on body size and temperature (Ugedal et al. 1992). Consequently, ^{137}Cs concentrations in fish reflect long-term feeding histories in the same sense as do other measures of body composition. Any correlation between ^{137}Cs and individual diet based on gut analysis would thus be difficult to detect because of the overall variability of diet and ^{137}Cs concentrations. Here, however, having a large amount of data available, we found significant relationships between individual diet and ^{137}Cs, even after accounting for size and species differences.

If individual specialization influences fish ^{137}Cs, as found here, this should be reflected in the population variance of ^{137}Cs. There was a tendency of increasing variance with trophic position. One explanation may be less integration of the prey ^{137}Cs variability in piscivores than in planktivores owing to the relatively lower number of ingested prey items of the former. A more plausible explanation is that the degree of omnivory, in principle, may increase with trophic

© 2005 NRC Canada

position as the number of trophic levels of potential prey increases. PerchBF and perchF that had higher variance but lower trophic position than pike obliterated the relationship between variance and trophic position. Both perchBF and perchF were feeding from two trophic levels, whereas pike were primarily piscivorous, suggesting that omnivory is better than trophic position for explaining the variance of ^{137}Cs or body composition in general. For comparison, the range in the stable isotopic composition of N among individual fish in Lake Geneva was too small to explain the large within-population variation of persistent chlorinated organics and Hg (Dufour et al. 2001). Stable N isotopes give information about trophic positions of consumers but not about contamination sources. Evidently, high contaminant variation can result from different food sources with similar trophic positions but different contamination levels, as we found for radiocesium in zooplankton and zoobenthos. Accordingly, the best correlation with the observed variance in Lake Flatsjön was provided by the functional omnivory index, which incorporates the prey ^{137}Cs level rather than prey trophic level. The most variable ^{137}Cs levels were found in perchBF with an average diet composed of about equal amounts of zoobenthos and fish, the resources that differed most in ^{137}Cs. We observed no correlation between Levins' index of niche width and ^{137}Cs variance. A high degree of omnivory, however, is not necessarily related to a wide population niche, as Levins' index can also increase with food diversity within a trophic level.

The awareness of individual resource specialization has recently increased and it appears to be a widespread phenomenon in lacustrine fish populations (see review by Bolnick et al. 2003). The significant relationships between individual diet and ^{137}Cs, together with the very good correlation between functional omnivory and the ^{137}Cs variance, suggest a causal and positive relationship between individual resource specialization and the within-population variance of trophically transferred contaminants. This view is supported by modeling studies showing that omnivory (Vander Zanden and Rasmussen 1996) or variation among individuals in prey contamination, i.e., functional omnivory (Madenjian et al. 1993, 1994), must be considered for explaining the observed variation of PCBs in salmonines. If the relationship between individual specialization and ^{137}Cs variability can be generalized to other systems and contaminants, it could provide a powerful tool for fish ecologists. An intriguing approach would be to investigate where and under what conditions individual resource specialization might be operating by comparing the variance of contaminants in fish with, e.g., lake productivity, lake size, habitat diversity, or species composition. Over the years, large amounts of fish contaminant data from a wide range of freshwater ecosystems have accumulated in publications and databases that could be utilized for such comparative studies.

In conclusion, for adequate assessment of the health risks associated with freshwater fish consumption, the sources and magnitude of the generally high variability of ^{137}Cs and other pollutants should be more carefully considered in monitoring and modeling of the fate of contaminants in lakes. Perch would be a suitable key species in monitoring programs: *Perca* species readily accumulate radiocesium and are circumpolarly distributed, often abundant, and can be caught during all seasons. In addition, perch species are widely popular as game and food and are thus potentially important for the transfer of radiocesium to humans. Our results may also have implications for food consumption estimates based on radiocesium. Individual diet differences can generate considerable variability in ^{137}Cs concentration within populations, whereas bioenergetic factors appear to be less important. This implies that bioenergetic modeling and established empirical equations that describe the Cs turnover in fish can be confidently used for estimating long-term feeding rates in situ, provided that individual diet is known (e.g., farmed fish or species with highly specialized feeding). However, for fish with a broad potential diet or undergoing ontogenetic diet shifts, researchers must be aware that the accuracy of tracer-derived consumption estimates may suffer from this additional source of variation, which is difficult to control or assess. Gut content is not a reliable predictor of long-term individual diet, and stable N isotope signatures may be misleading because contaminant concentrations as well as N isotopic ratios can vary among prey within a trophic level.

Acknowledgements

We thank Åsa Sjöblom, Sebastian Sobek, and Susanna Vesterberg for help in the field or laboratory and Peter Eklöv and two anonymous referees for valuable comments on the manuscript. The Swedish Radiation Protection Authority (Statens strålskyddsinstitut, SSI) and the Nordic Nuclear Safety Research (Nordisk kärnsäkerhetsforskning, NKS) provided financial support.

References

Agresti, A. 1996. An introduction to categorical data analysis. Wiley, New York.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., and Forister, M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. Am. Nat. **161**: 1–28.

Broberg, A., Malmgren, L., and Jansson, M. 1995. Relations between resuspension and the content of ^{137}Cs in freshwater fish in some Swedish lakes. J. Aquat. Ecosyst. Health, **4**: 285–294.

Dufour, E., Gerdeaux, D., Corvi, C., Khim-Heang, S., and Mariotti, A. 2001. Assessment of the contaminant concentration variability among Lake Geneva arctic char using stable isotopic composition (∂^{15}N and ∂^{13}C). Environ. Toxicol. **16**: 185–191.

Elliott, J.M., Hilton, J., Rigg, E., Tullett, P.A., Swift, D.J., and Leonard, D.R.P. 1992. Sources of variation in post-Chernobyl radiocaesium in fish from two Cumbrian lakes (north-west England). J. Appl. Ecol. **29**: 108–119.

Forseth, T., Jonsson, B., Næumann, R., and Ugedal, O. 1992. Radioisotope method for estimating food consumption by brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. **49**: 1328–1335.

Gingras, J., and Boisclair, D. 2000. Comparison between consumption rates of yellow perch (*Perca flavescens*) estimated with a digestive tract model and with a radioisotope approach. Can. J. Fish. Aquat. Sci. **57**: 2547–2557.

Greenfield, B.K., Hrabik, T.R., Harvey, C.J., and Carpenter, S.R. 2001. Predicting mercury levels in yellow perch: use of water chemistry, trophic ecology, and spatial traits. Can. J. Fish. Aquat. Sci. **58**: 1419–1429.

© 2005 NRC Canada

Hadderingh, R.H., van Aerssen, G.H.F.M., Ryabov, I.N., Koulikov, A.O., and Belova, N. 1997. Contamination of fish with ^{137}Cs in Kiev reservoir and old river bed of Pripyat near Chernobyl. *In* Freshwater and estuarine radioecology. *Edited by* G. Desmet, P. J. Blust, R.N.J. Comans, J.A. Fernandez, J. Hilton, and A. de Bettencourt. Elsevier Science Publishers B.V., Amsterdam. pp. 339–351.

Håkanson, L. 1999. A compilation of empirical data and variations in data concerning radiocesium in water, sediments and fish in European lakes after Chernobyl. *J. Environ. Radioact.* **44**: 21–42.

Håkanson, L., Andersson, T., and Nilsson, Å. 1992. Radioactive caesium in fish in Swedish lakes 1986–1988 — general pattern related to fallout and lake characteristics. J. Environ. Radioact. **15**: 207–229.

Häsänen, E., Kolehmainen, S., and Miettinen, J.K. 1967. Biological half-time of ^{137}Cs in three speices of freshwater fish: perch, roach and rainbow trout. *In* Radioecological concentration processes. *Edited by* B. Åberg and F.P. Hungate. Pergamon Press, Oxford. pp. 921–924.

Holloman, K.A., Dallas, C.E., Brisbin, I.L., Jr., and Jagoe, C.H. 1997. Spatial and temporal patterns of radiocesium contamination in mosquitofish, *Gambusia holbrooki* (Girard, 1859), inhabiting a nuclear reactor cooling reservoir. J. Environ. Radioact. **35**: 243–259.

Kennedy, B.P., Klaue, B., Blum, J.D., and Folt, C.L. 2004. Integrative measures of consumption rates in salmon: expansion and application of a trace element approach. J. Appl. Ecol. **41**: 1009–1020.

Kidd, K.A., Bootsma, H.A., Hesslein, R.H., Muir, D.C.G., and Hecky, R.E. 2001. Biomagnification of DDT through the benthic and pelagic food webs of Lake Malawi, East Africa: importance of trophic level and carbon source. Environ. Sci. Technol. **35**: 14–20.

Kolehmainen, S.E. 1972. The balances of ^{137}Cs, stable cesium and potassium of bluegill (*Lepomis macrochirus* Raf.) and other fish in White Oak Lake. Health Phys. **23**: 301–315.

Kolehmainen, S.E., Häsänen, E., and Miettinen, J.K. 1967. ^{137}Cs in fish, plankton and plants in Finnish lakes during 1964–5. *In* Radioecological concentration processes. *Edited by* B. Åberg and F.P. Hungate. Pergamon Press, Oxford. pp. 913–919.

Kulikov, N.V., and Kulikova, V.G. 1977. Accumulation of ^{90}Sr and ^{137}Cs by certain freshwater fish under natural conditions. Ekologiya, **5**: 45–49.

Le Cren, E.D. 1951. The length–weight relationship and seasonal cykle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. **20**: 201–219.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, N.J.

Liebscher, K., and Smith, H. 1968. Essential and nonessential trace elements. Arch. Environ. Health, **17**: 881–890.

Madenjian, C.P., Carpenter, S.R., Eck, G.W., and Miller, M.A. 1993. Accumulation of PCBs by lake trout (*Salvelinus namaycush*): an individual-based model approach. Can. J. Fish. Aquat. Sci. **50**: 97–109.

Madenjian, C.P., Carpenter, S.R., and Rand, P.S. 1994. Why are the PCB concentrations of salmonine individuals from the same lake so highly variable? Can. J. Fish. Aquat. Sci. **51**: 800–807.

McCreedy, C.D., Jagoe, C.H., Glickman, L.T., and Brisbin, I.L., Jr. 1997. Bioaccumulation of ^{137}Cs in yellow bullhead catfish (*Ameiurus natalis*) inhabiting an abandoned nuclear reactor reservoir. Environ. Toxicol. Chem. **16**: 328–335.

Meili, M. 1991. In situ assessment of trophic levels and transfer rates in aquatic food webs, using chronic (Hg) and pulsed (Chernobyl ^{137}Cs) environmental contaminants. Verh. Int. Ver. Limnol. **24**: 2970–2975.

Newman, M.C., and Brisbin, I.L.J. 1990. Variation of ^{137}Cs levels between sexes, body sizes and collection localities of mosquitofish, *Gambusia holbrooki* (Girard 1859), inhabiting a reactor cooling reservoir. J. Environ. Radioact. **12**: 131–142.

Oleksyk, T.K., Gashchak, S.P., Glenn, T.C., Jagoe, C.H., Peles, J.D., Purdue, J.R., Tsyusko, O.V., Zalissky, O.O., and Smith, M.H. 2002. Frequency distributions of ^{137}Cs in fish and mammal populations. J. Environ. Radioact. **61**: 55–74.

Pinder, J.E.I., and Giesy, J.P. 1981. Frequency distributions of the concentrations of the essential and nonessential elements in largemouth bass, *Micropterus salmoides*. Ecology, **62**: 456–468.

Power, M., Klein, G.M., Guiguer, K., and Kwan, M.K.H. 2002. Mercury accumulation in the fish community of a sub-Arctic lake in relation to trophic position and carbon sources. J. Appl. Ecol. **39**: 819–830.

Rowan, D.J., and Rasmussen, J.B. 1994. Bioaccumulation of radiocesium by fish: the influence of physicochemical factors and trophic structure. Can. J. Fish. Aquat. Sci. **51**: 2388–2410.

Rowan, D.J., and Rasmussen, J.B. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (^{137}Cs). Can. J. Fish. Aquat. Sci. **53**: 734–745.

Rowan, D.J., Chant, L.A., and Rasmussen, J.B. 1998. The fate of radiocesium in freshwater communities — why is biomagnification variable both within and between species? J. Environ. Radioact. **40**: 15–36.

SAS Institute Inc. 2000. JMP statistics and graphics guide. Version 4. SAS Institute Inc., Cary, N.C.

Saxén, R., Rissanen, K., and Koskelainen, U. 2002. Distribution of ^{137}Cs in tissues and organs of fishes from Finnish lakes and the Baltic Sea. *In* Proceedings from the International Conference on Radioactivity in the Environment. *Edited by* P. Strand, P. Børretsen, and T. Jølle. CD appendix. Norwegian Radiation Protection Authority, Østerås, Norway.

Sherwood, G.D., Kovecses, J., Hontela, A., and Rasmussen, J.B. 2002. Simplified food webs lead to energetic bottlenecks in polluted lakes. Can. J. Fish. Aquat. Sci. **59**: 1–5.

Smith, J.T., Comans, R.N.J., Beresford, N.A., Wright, S.M., Howard, B.J., and Camplin, W.C. 2000. Pollution — Chernobyl's legacy in food and water. Nature (London), **405**: 141–141.

Sonesten, L. 2001. Land use influence on ^{137}Cs levels in perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* L.). J. Environ. Radioact. **55**: 125–143.

Sundbom, M., Meili, M., Andersson, E., Östlund, M., and Broberg, A. 2003. Long-term dynamics of Chernobyl ^{137}Cs in freshwater fish: quantifying the effect of body size and trophic level. J. Appl. Ecol. **40**: 228–240.

Thomann, R.V. 1981. Equilibrium model of fate of microcontaminants in diverse aquatic food chains. Can. J. Fish. Aquat. Sci. **38**: 280–296.

Tucker, S., and Rasmussen, J.B. 1999. Using ^{137}Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) in the field. Can. J. Fish. Aquat. Sci. **56**: 875–887.

Tucker, S., Pazzia, I., Rowan, D., and Rasmussen, J. 1999. Detecting pan-Atlantic migration in salmon (*Salmo salar*) using ^{137}Cs. Can. J. Fish. Aquat. Sci. **56**: 2235–2239.

Ugedal, O., Jonsson, B., Njåstad, O., and Næumann, R. 1992. Effects of temperature and body size on radiocaesium retention in brown trout, *Salmo trutta*. Freshw. Biol. **28**: 165–171.

Ugedal, O., Forseth, T., Jonsson, B., and Njåstad, O. 1995. Sources of variation in radiocaesium levels between individual fish from a Chernobyl contaminated Norwegian lake. J. Appl. Ecol. **32**: 352–361.

© 2005 NRC Canada

Vander Zanden, M.J., and Rasmussen, J.B. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. Ecol. Monogr. **66**: 451–477.

Wauters, J., Vidal, M., Elsen, A., and Cremers, A. 1996. Prediction of solid/liquid distribution coefficients of radiocaesium in soils and sediments. Part two: a new procedure for solid phase speciation of radiocaesium. Appl. Geochem. **11**: 595–599.

Western, J.R.H., and Jennings, J.B. 1970. Histochemical demonstration of hydrochloric acid in the gastrictubules of teleosts using an *in vivo* prussian blue technique. Comp. Biochem. Physiol. **35**: 879–884.

Whicker, F.W., Hinton, T.G., and Niquette, D.J. 1997. Effects of a partial drawdown on the dynamics of ^{137}Cs in an abandoned reactor cooling reservoir. *In* Freshwater and estuarine radioecology. *Edited by* G. Desmet, R.J. Blust, R.N.J. Comans, J.A. Fernandez, J. Hilton, and A. de Bettencourt. Elsevier Science Publishers B.V., Amsterdam. pp. 193–202.

Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Upper Saddle River, N.J.

© 2005 NRC Canada

Influence of land use on fine sediment in salmonid spawning gravels within the Russian River Basin, California

Jeff J. Opperman, Kathleen A. Lohse, Colin Brooks, N. Maggi Kelly, and Adina M. Merenlender

Abstract: Relationships between land use or land cover and embeddedness, a measure of fine sediment in spawning gravels, were examined at multiple scales across 54 streams in the Russian River Basin, California. The results suggest that course-scale measures of watershed land use can explain a large proportion of the variability in embeddedness and that the explanatory power of this relationship increases with watershed size. Agricultural and urban land uses and road density were positively associated with embeddedness, while the opposite was true for forest cover. The ability of land use and land cover to predict embeddedness varied among five zones of influence, with the greatest explanatory power occurring at the entire-watershed scale. Land use within a more restricted riparian corridor generally did not relate to embeddedness, suggesting that reach-scale riparian protection or restoration will have little influence on levels of fine sediment. The explanatory power of these models was greater when conducted among a subset of the largest watersheds (maximum $r^2 = 0.73$) than among the smallest watersheds (maximum $r^2 = 0.46$).

Résumé : Nous avons examiné à plusieurs échelles les relations entre l'utilisation des terres et la couverture végétale, d'une part, et le colmatage du substrat, une mesure des sédiments fins dans les graviers de reproduction, d'autre part, dans 54 cours d'eau du bassin versant de la rivière Russian, Californie. Nos résultats indiquent que des évaluations de l'utilisation des terres dans le bassin versant à une échelle grossière peuvent expliquer une proportion importante de la variabilité du colmatage et que le pouvoir explicatif de cette relation augmente en fonction de la taille du bassin versant. Il y a une association positive entre les utilisations urbaine et agricole des terres et la densité des routes, d'une part, et le colmatage, d'autre part, alors que la relation est inverse dans le cas de la couverture forestière. Le potentiel de l'utilisation des terres et de la couverture végétale pour prédire le colmatage varie en fonction des cinq zones d'influence et le potentiel maximal se manifeste à l'échelle du bassin versant entier. Il n'y a pas généralement de corrélation entre l'utilisation des terres sur un corridor plus étroit le long des rives et le colmatage, ce qui laisse croire que la restauration ou la protection des rives au niveau de la section du cours d'eau aura peu d'influence sur les quantités de sédiments fins. Le pouvoir explicatif de ces modèles est plus grand lorsqu'il s'applique à un sous-ensemble des bassins versants les plus grands (r^2 maximal = 0,73) plutôt qu'aux plus petits bassins versants (r^2 maximal = 0,46).

[Traduit par la Rédaction]

Introduction

In California, coastal watersheds once supported prodigious runs of six species of anadromous salmonids: coho (*Oncorhynchus kisutch*), Chinook (*Oncorhynchus tshawytscha*), pink (*Oncorhynchus gorbuscha*), and chum salmon (*Oncorhynchus keta*), and steelhead (*Oncorhynchus mykiss*) and sea-run coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) (Moyle 2002). At present, many of these runs have been extirpated from coastal drainages (e.g., pink and chum salmon from the Russian River Basin), while those that remain are generally listed as threatened or endangered under the Federal Endangered Species Act (Mills et al. 1997; Busby et al. 2000; Weitkamp et al. 2000).

Because degradation of freshwater habitat is one of the key factors leading to the decline of anadromous fish along the Pacific coast of the United States (Nehlsen et al. 1991; National Research Council 1996; Nehlsen 1997), resources and attention devoted to stream restoration have greatly increased, and millions of dollars are currently being spent to restore fish habitat (Roper et al. 1997; Roni et al. 2002). In particular, sedimentation has been identified as one possible

Received 23 July 2004. Accepted 4 July 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 28 October 2005.
J18233

J.J. Opperman,[1,2] K.A. Lohse, N.M. Kelly, and A.M. Merenlender. Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3110, USA.
C. Brooks. University of California's Integrated Hardwood Range Management Program, North Coast Research and Extension Group, 4070 University Road, Hopland, CA 95449, USA.

[1]Corresponding author (e-mail: jopperman@ucdavis.edu).
[2]Present address: Center for Integrated Watershed Science and Management, University of California, Davis, CA 95616, USA.

 doi: 10.1139/F05-187 © 2005 NRC Canada

agent degrading freshwater ecosystems and limiting the persistence and recovery of salmonid populations. High levels of fine sediment (<2 mm diameter) in spawning gravels are correlated with low survival of salmonid eggs and alevins (Everest et al. 1987; Reiser and White 1988; Kondolf 2000). Further, high levels of fine sediment can simplify bed features, reduce cover and populations of macroinvertebrates, and fill pools (Henley et al. 2000; McIntosh et al. 2000; Suttle et al. 2004).

Land-use activities that alter or replace native vegetation are considered key drivers leading to increased sediment production and delivery to streams (Waters 1995; Pimentel and Kounang 1998). Numerous studies have found that land-use activities such as agriculture, grazing, roads, and urban development can lead to elevated sediment production, both directly (e.g., rill and gully erosion) and indirectly (reduced infiltration leading to higher peak flows and channel degradation) (Swanson and Dyrness 1975; Montgomery 1994; Pizzuto et al. 2000). While these studies identify the mechanisms by which land-use activities produce sediment, methods to predict characteristics of in-stream sediment (e.g., magnitude of fluxes, grain size) based on patterns of watershed land use remain limited in scope, scale, and explanatory power (Nilsson et al. 2003). Given these limitations, it has been suggested that a promising alternative is to build empirical relationships between land use and observed sediment fluxes or concentrations (Nilsson et al. 2003).

An important issue that has emerged with empirical modeling is the spatial scaling of variables (Allan et al. 1997; Allan and Johnson 1997; Strayer et al. 2003). Recent research has explored linkages between land use and aquatic habitat at various scales (Hunsaker and Levine 1995; Lammert and Allan 1999; Strayer et al. 2003), including levels of fine sediment in streams (Richards et al. 1996; Wohl and Carline 1996; Snyder et al. 2003) and indices of salmonid abundance (Paulsen and Fisher 2001; Pess et al. 2002; Regetz 2003). These studies have reached conflicting conclusions regarding the spatial scale (or zone of influence) at which land use can predict effectively the ecological response of the stream reach. For example, several studies have concluded that land use within the local area (e.g., the riparian corridor surrounding or immediately upstream of a site) has a greater influence on the freshwater ecosystem than land use within the entire watershed (Jones et al. 1999; Lammert and Allan 1999; Sponseller et al. 2001), while other studies have come to the opposite conclusion (Omernik et al. 1981; Roth et al. 1996; Wang et al. 1997). Differences in the size of watersheds examined by these studies may have contributed to their different conclusions on the effects of land use on aquatic ecosystems. By elucidating the scales at which land use influences habitat, research on land use across scales can help managers target their restoration and management efforts to the appropriate scale.

Nearly all research on the influence of land use across scales has been concentrated in the eastern and midwestern United States (US). Further, in the western US, the research available to inform restoration programs for anadromous fish has been largely conducted in the conifer-dominated watersheds of the Pacific Northwest. Conversely, very little research on salmonid habitat has occurred within the hardwood-dominated, Mediterranean-climate watersheds of northern and central California. These watersheds have much more rugged topography than those studied in the eastern and midwestern US and different vegetation and hydrologic regimes and more varied land uses than those found in the Pacific Northwest. Therefore, generalizations about scales of influence and the role of land use developed in other regions may not be able to be directly transferred to Mediterranean-climate watersheds. An understanding of the basic processes that shape habitat, and the scales at which they operate, can help the adaptation of restoration strategies to this region.

This paper examines the empirical relationship between land use and land cover (LULC) and the level of fine sediment in spawning gravels across 54 streams in a Mediterranean-climate basin in northern California. Specifically, we ask the following questions. (*i*) Can readily available data on land use help explain the patterns of fine sediment found in streams across this basin? (*ii*) Within what zone of influence, ranging from the local riparian corridor to the entire watershed, does land use have the most explanatory power for predicting levels of fine sediment and what accounts for these differences in explanatory power? (*iii*) What is the effect of watershed size on the predictive power of these empirical relationships? This last question is motivated by the work of Strayer et al. (2003), who concluded that the ability of LULC patterns to explain in-stream variables became weaker in smaller watersheds (e.g., <1000 ha). Thus we examine the influence of spatial scale in two different ways: within watersheds (i.e., zone of influence) and across watersheds (e.g., large watersheds vs. small watersheds).

Materials and methods

Study region

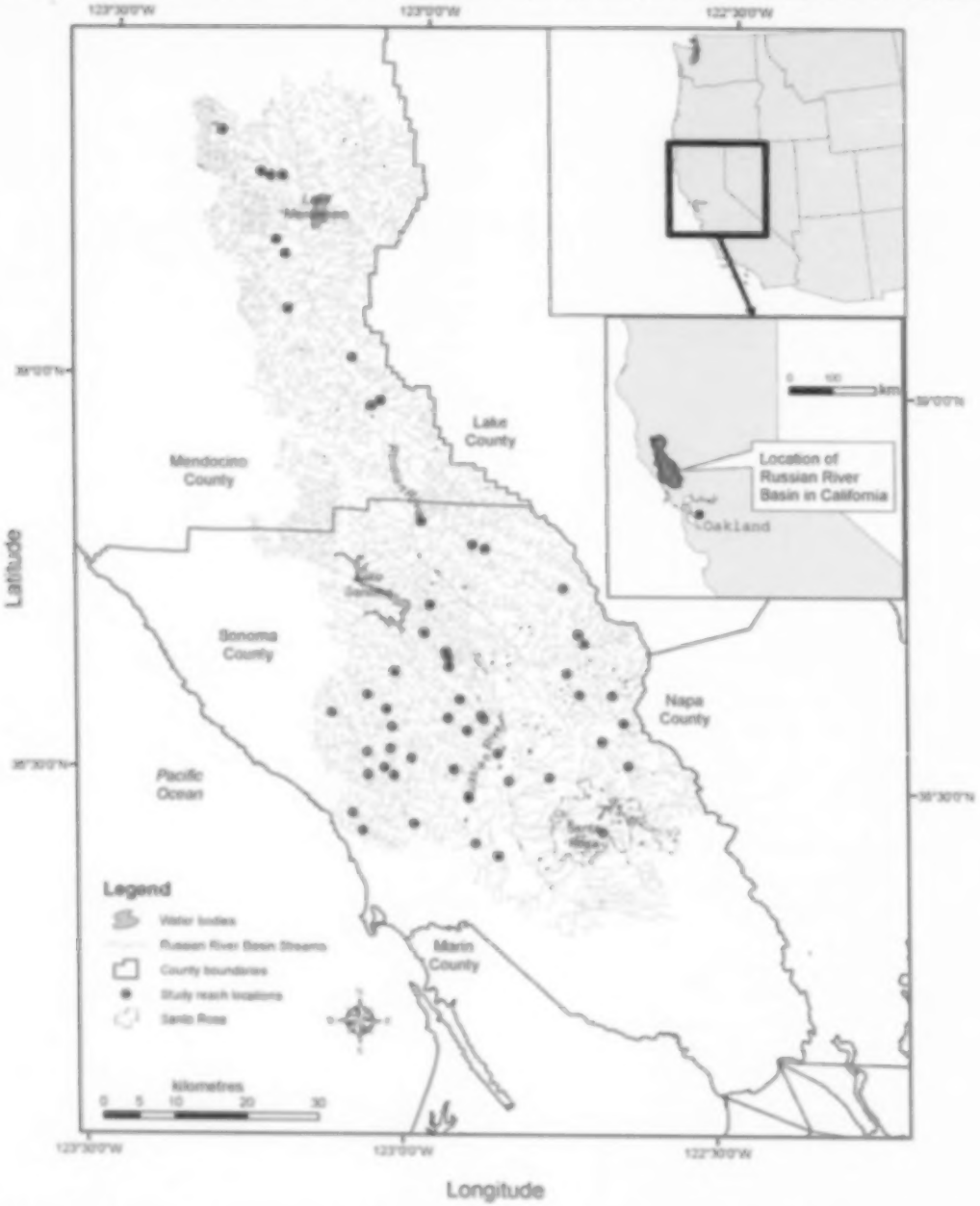
The Russian River Basin is located in northwestern California within Sonoma and Mendocino counties (Fig. 1). The basin is currently listed as impaired by sediment under Section 303(*d*) of the Federal Clean Water Act. The basin also provides habitat for several species of anadromous fish, including Chinook and coho salmon and steelhead trout. All three runs are currently listed under the Federal Endangered Species Act as being threatened or endangered.

The mainstem Russian River flows for approximately 175 km within a 3850-km^2 basin that is underlain primarily by the Jurassic–Cretaceous age Franciscan Formation. Elevations range from sea level to 1325 m. The basin has a Mediterranean climate with cool, wet winters and hot, dry summers (Gasith and Resh 1999); the mean annual rainfall ranges from 69 cm to as high as 216 cm across the subbasins, with the majority of precipitation between December and March and little or no rain between May and October.

The majority of the basin is dominated by hardwood forests, oak savannas, chaparral, and grasslands. Conifer-dominated forests occur near the coast and intermittently throughout the basin on north-facing slopes. Land use is varied and includes vineyards, orchards, and other agriculture, sheep and cattle grazing, timber harvest, and urban, suburban, and low-density rural residential housing. Vineyards, urban areas, and suburban developments dominate the valley floors. Currently, there are high rates of land-use change on the hillslopes with conversion from natural vegetation to vineyard and low-density residential development (Meren-

© 2005 NRC Canada

Fig. 1. Location of 54 stream reaches in the Russian River Basin (California, USA) surveyed for levels of fine sediment in spawning gravels.



lender et al. 1998; Heaton and Merenlender 2000; Merenlender 2000).

In-stream habitat data were collected by the California Department of Fish and Game (CDFG) in the Russian River Basin between 1997 and 2000 (Fig. 1). Field crews recorded the concentration or level of fine sediment within gravel and cobble substrate, termed "embeddedness", at each potential spawning site on a four-level ordinal scale, from 1 (very low levels of fine sediment) to 4 (very high levels of fine sediment). Through dynamic segmentation and calibration (Radko 1997), we spatially linked reach-scale data to a drainage network within a geographic information system (GIS) and, using a 10-m digital elevation model (DEM), calculated stream gradients.

From the embeddedness data we calculated an embeddedness index (EI) for each surveyed reach by subtracting the proportion of spawning sites with very low embeddedness (level 1) from those with very high embeddedness (level 4). Thus, the index can range from negative 100 (all units have embeddedness value 1) to 100 (all units have embeddedness

© 2005 NRC Canada

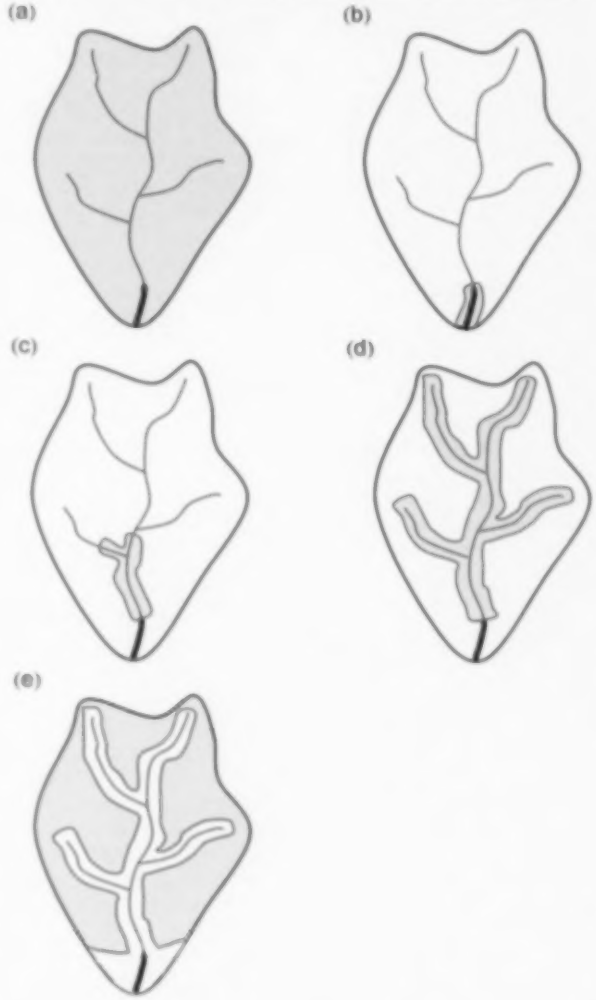
value 4). By considering only the endpoints of this scale (i.e., the extreme values of 1 and 4), we reduced the error inherent in an essentially qualitative ranking score while still allowing for maximal spread in the response variable. To determine how much information was lost by using only the endpoints of the scale, we also calculated a weighted average embeddedness for each reach that used all embeddedness values.

Analyses were restricted to reaches with at least 10 samples of embeddedness (mean = 47 samples) and a low gradient (<3%) likely to show a depositional response to sediment supply (Montgomery and Buffington 1993). For each of the 54 reaches meeting these criteria, we used the DEM and the ArcView (ESRI, Redlands, California) extension FlowZones to derive a watershed above the downstream end of each surveyed reach. We also used the DEM to derive slope classes for the watersheds.

Explanatory variables were obtained from several sources and entered into the GIS. For LULC, we used a California Vegetation data layer derived from 1994 Landsat TM with a 1-ha minimum mapping unit (California Department of Forestry Land Cover Mapping and Monitoring Program). We used aggregated LULC categories of agriculture (row crops, vineyards, and orchards), herbaceous (annual grasslands), forest (including hardwood, conifer, and mixed evergreen forests), shrubs (generally chaparral), and urban. Road density was calculated by summing the lengths of the 1:100 000 scale US Census Bureau TIGER 2000 roads and dividing that sum by the size of the area of analysis (km road-km^{-2} area). For geology, we used the 1:750 000 GIS data for the Geologic Map of California (California Geographic Survey).

We quantified the amount of all LULC, geology, and road density variables within five zones of influence (Fig. 2). The "watershed" zone included all areas that drained into the downstream end of each reach. For the "local" zone, we delineated the area surrounding each reach at two different distances (30 m and 60 m) from the stream banks using the GIS buffering tool. These two distances provided essentially identical information, so subsequent analyses include only the 30-m riparian buffer. For the "upstream" zone, we buffered the riparian corridor by 30 m on each side of the stream 1 km upstream of the upper end of each surveyed reach. We then used the DEM to create a stream network upstream of each reach, with headwater channels initiating at a drainage area of 2 ha. This "network" zone was then buffered by 30 m. Our objective with this routine was to capture all drainage pathways, including intermittent and ephemeral channels, not captured by standard maps of "blue-line" streams (Hansen 2001). The contributing area for defining channel initiation is likely conservative based on field studies in the region (Montgomery and Dietrich 1988). Finally, we defined the "hillslope" zone of influence as the area that remained after subtracting the area of the network zone from the area of the watershed zone. Thus this zone evaluates the influence of land cover not directly adjacent to the densified channel network on patterns of stream sediment.

Fig. 2. Conceptual maps showing the five zones of influence within a hypothetical watershed: (*a*) watershed, (*b*) local, (*c*) upstream, (*d*) network, and (*e*) hillslope. The thick line represents the focal reach (i.e., the reach in which embeddedness data were collected), and the shaded area represents the portion of the watershed included in the analysis for a given zone of influence.



Data analysis

We initially plotted the distribution of values for the embeddedness index across three groups of watersheds that varied in the amount of land classified in a category indicating development (i.e., either urban or agriculture): no land classified as developed, low development (1%–5% of land classified as developed), or moderate to high development (>5% developed). We then used simple linear regression to explore the relationships between single explanatory variables and the embeddedness index for the five zones of influence within all 54 watersheds. Explanatory variables with non-normal distributions were transformed to improve the homoscedasticity of residuals. For example, the proportion of zones of influence in agriculture and urban land uses were cube-root transformed. We then used stepwise regression to develop multiple regression models. We based our final model selection on the adjusted r^2 (r^2_{adj}) and significance of the coefficients. We interpreted individual regression co-

© 2005 NRC Canada

efficients from the multiple regression analyses with caution because moderate correlation occurred between potential predictors at the various scales.

In addition to these analyses, we evaluated the influence of size of the watershed on the predictive power of the models. We categorized the watersheds by size into three classes (n = 18 per class): small watersheds (<1000 ha), intermediate watersheds (1000–3400 ha), and large watersheds (3400 – 22 000 ha). We repeated a subset of these analyses after removing those watersheds in which timber harvest is likely a major influence, because our data could not adequately address the potential influence of current and historic timber harvest (e.g., our classification for forest did not differentiate among an old-growth forest, one that had been cut 100 years ago, and one that had been cut 20 years ago). The eliminated watersheds had more than 10% of the land under a Timber Harvest Plan (THP) with the California Department of Forestry.

Results

Explanatory variables showed moderate levels of correlation (Table 1). For example, forest cover was negatively correlated with agriculture, while road density was positively correlated with urban land cover and somewhat correlated with agricultural land cover. The proportion of sedimentary geology was positively correlated with agriculture (correlation coefficient = 0.89) and negatively correlated with forest (–0.50). Proportions of a specific land cover (e.g., agriculture) at the watershed zone of influence were highly correlated with the network (correlation coefficient >0.90) and hillslope (>0.98) zones and less strongly correlated with the local zone. Correlations between watershed and local LULC were higher within small watersheds (agriculture = 0.50, forest = 0.49) than they were for the large watersheds (agriculture = 0.35, forest = 0.17).

The three size classes of watersheds contained different distributions of LULC proportions for the land covers most associated with sediment production in the study region — urban and agricultural. The intermediate watersheds contained very little urban area and the smallest watersheds had no urban areas. The largest and smallest watersheds had somewhat similar distributions of agriculture (in terms of interquartile range and maximum), while the intermediate watersheds had very little agriculture (Fig. 3*a*). However, the distribution for road density was very similar among the three size groups (Fig. 3*b*).

The distribution of EI values varied considerably among groups of watersheds that had no area classified as developed (EI = –12 ± 7 (mean ± standard error), median = –22), those that had between 1% and 5% developed (6 ± 10, median = 0) and those that had greater than 5% developed (43 ± 9, median = 35) (Fig. 4). The stream with the highest EI in the no-development group has had recent timber harvest activity (Fig. 4*a*).

Linear regression analyses showed that the amount of agriculture and road density were consistently positively associated with EI and the amount of forest cover was consistently negatively associated with EI, across zones of influence and for different size groups of watersheds (Table 2 and Fig. 5*a*). However, LULC variables were rarely significant

Table 1. Coefficients of correlation between explanatory variables for the watershed zone of influence for all 54 watersheds.

	Agriculture	Urban	Herbaceous	Shrub	Forest	Road density	Volcanic	Franciscan	Sedimentary	Low relief	High relief
Agriculture		0.23	–0.12	–0.06	**–0.63**	**0.52**	0.10	**–0.32**	**0.89**	**0.85**	**–0.78**
Urban	0.23		**0.30**	–0.16	**–0.40**	**0.60**	0.10	**–0.30**	**0.28**	**0.58**	**–0.48**
Herbaceous	–0.12	**0.30**		**–0.28**	–0.25	0.02	0.18	0.08	–0.03	0.19	**–0.31**
Shrub	–0.06	–0.16	**–0.28**		**–0.52**	–0.17	0.20	0.27	–0.19	–0.12	0.06
Forest	**–0.63**	**–0.40**	–0.25	**–0.52**		**–0.37**	**–0.33**	0.05	**–0.50**	**–0.70**	**0.73**
Road density	**0.52**	**0.60**	0.02	–0.17	**–0.37**		–0.02	–0.15	**0.60**	**0.69**	**–0.67**
Volcanic	0.10	0.10	0.18	0.20	**–0.33**	–0.02		**–0.39**	–0.09	0.22	**–0.33**
Franciscan	**–0.32**	**–0.30**	0.08	0.27	0.05	–0.15	**–0.39**		–0.27	**–0.33**	**0.28**
Sedimentary	**0.89**	**0.28**	–0.03	–0.19	**–0.50**	**0.60**	–0.09	–0.27		**0.80**	**–0.72**
Low relief	**0.85**	**0.58**	0.19	–0.12	**–0.70**	**0.69**	0.22	**–0.33**	**0.80**		**–0.95**
High relief	**–0.78**	**–0.48**	**–0.31**	0.06	**0.73**	**–0.67**	**–0.33**	**0.28**	**–0.72**	**–0.95**	

Notes: Low relief, the proportion of the watershed with slopes <10%; high relief, the proportion of the watershed with slopes >30%. Correlation coefficients in bold are statistically significant at $p \leq 0.05$.

© 2005 NRC Canada

Fig. 3. Distribution of explanatory variables for three size groups of watersheds (n = 18 for each; ×, median; brackets, interquartile range; △, maximum): (*a*) proportion agriculture (transformed as cube root of proportion agriculture to improve normality); (*b*) road density.

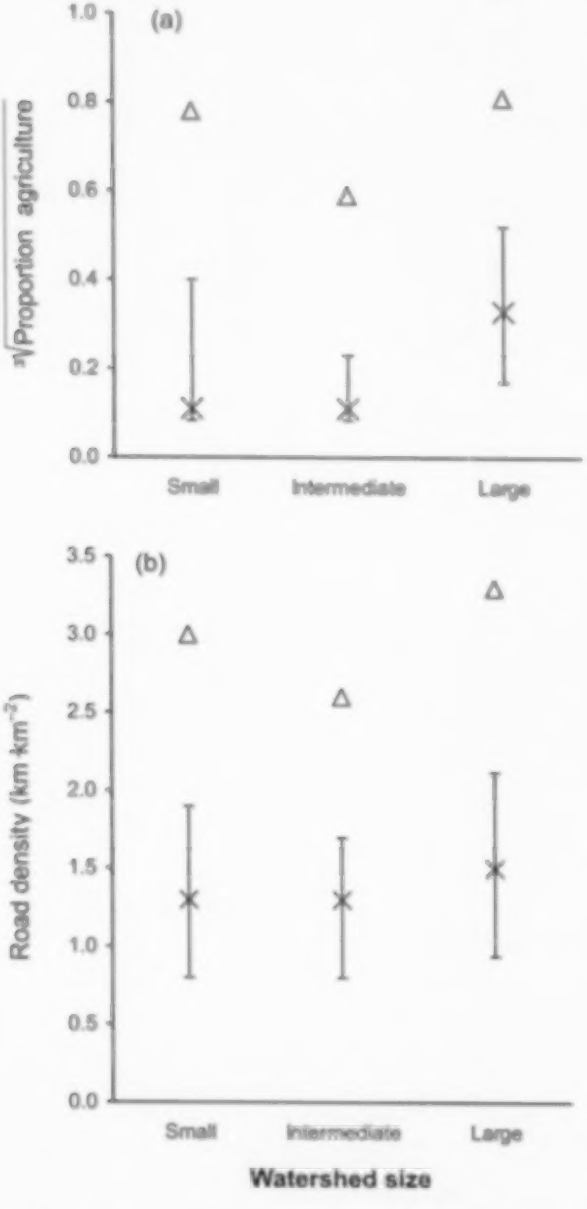
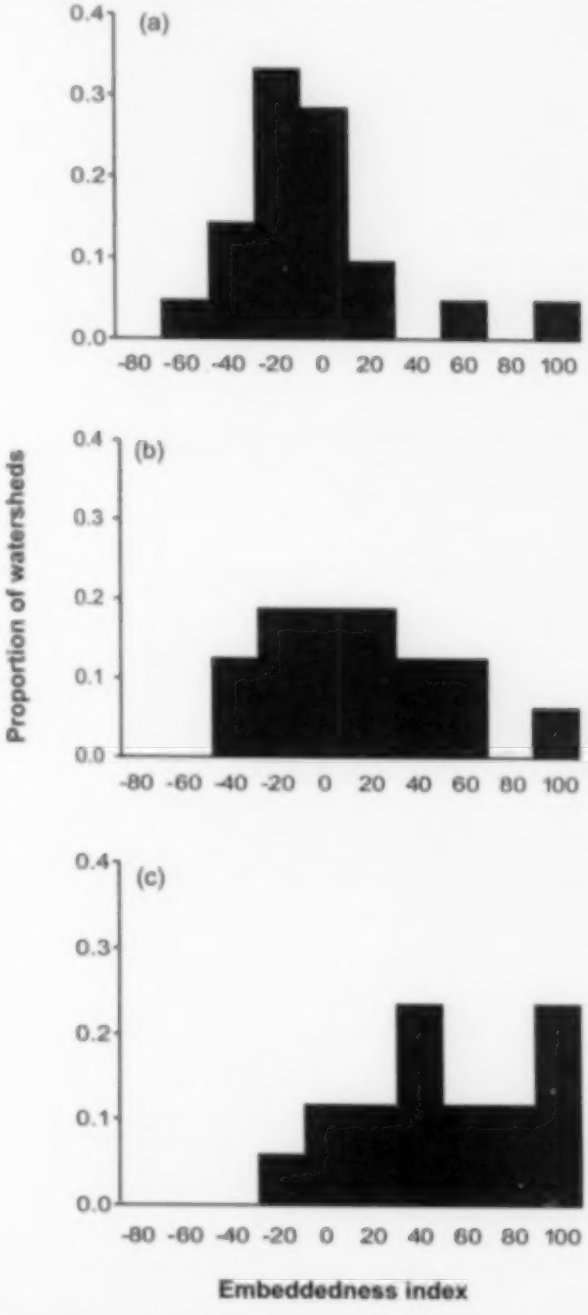


Fig. 4. Distributions of embeddedness index values among watersheds with (*a*) no development (defined as agricultural and urban land cover; n = 21); (*b*) 1%–5% developed (n = 16); and (*c*) >5% developed (n = 17).



within the local zone of influence (Table 2 and Fig. 5*b*). When urban land cover had a significant relationship with EI, the relationship was always positive (Table 2). Several of these relationships were stronger among the largest watersheds than among the intermediate and smallest watersheds. For example, while agriculture was significantly positively related to EI among all three size groups, the r^2 for the largest watersheds was 0.53 compared with 0.21 among the intermediate watersheds and 0.35 among the smallest watersheds. When one probable outlier was removed, the explanatory power (r^2) for agriculture increased to 0.75 for the largest watersheds (Fig. 5*a*). While this watershed had very little intensive agriculture, it had the highest proportion

© 2005 NRC Canada

Table 2. Linear regression results for analyses between land use – land cover variables and embeddedness index in streams in the Russian River Basin.

	Watershed coefficient	r^2	Local coefficient	r^2	Upstream coefficient	r^2	Network coefficient	r^2	Hillslope coefficient	r^2
All										
Agriculture*	95	0.29	44	0.12	60	0.15	94	0.25	82	0.22
Urban*	141	0.25			44	0.07			162	0.23
Road density	31	0.31			4	0.09	26	0.27	30	0.29
Forest	−102	0.21	−61	0.17	−56	0.15	−99	0.18	−78	0.13
Largest										
Agriculture*	128	0.53					96	0.29	97	0.38
Urban*	162	0.57							178	0.57
Road density	108	0.58					34	0.51	41	0.63
Forest	−175	0.54			−68	0.30	−171	0.54	−150	0.45
Intermediate										
Agriculture*	118	0.21					116	0.23		
Road density	96	0.33							35	0.26
Smallest										
Agriculture*	71	0.35			84	0.49	88	0.36	59	0.23
Forest	−81	0.27								

Note: Analyses were run for five within-watershed scales (i.e., zones of influence) and among four groups of watersheds: all 54 and three size groups (smallest, intermediate, and largest watersheds; $n = 18$ per group). Only results that were significant at the $p \leq 0.05$ level are displayed. Variables denoted with an asterisk (*) were transformed to improve normality by taking the cube root of the value.

urban and highest road density of all 54 watersheds. For the most part, geological variables were not correlated with EI. However, the proportion of sedimentary geology was positively and significantly correlated with EI for the watershed, hillslope, and network zones of influence.

Comparing the multiple regression models for each zone of influence for the full set of 54 reaches, the model for watershed had the greatest explanatory power ($r^2_{adj} = 0.42$), followed by network ($r^2_{adj} = 0.32$) and hillslope ($r^2_{adj} = 0.29$; Fig. 6). The local zone of influence had the lowest explanatory power ($r^2_{adj} = 0.07$). Geological variables were not selected within the multiple regression models. Stepwise regression consistently selected proportion agriculture as a significant model term, with a positive relationship with EI, for all zones of influence with the exception of local.

The size of the watershed influenced the predictive power of the empirical models, with explanatory power decreasing from larger to smaller watersheds (Fig. 6). The largest watersheds displayed trends similar to those for all watersheds combined, with the watershed zone having the greatest explanatory power ($r^2_{adj} = 0.73$), followed closely by network ($r^2_{adj} = 0.70$) and hillslope ($r^2_{adj} = 0.65$). The upstream zone had much lower explanatory power, and the local zone had almost no explanatory power. Within these models, terms for agriculture, road density, urban, and herbaceous had positive relationships with EI, while forest and shrub had negative relationships with EI.

The smallest watersheds displayed a different trend, with the upstream zone having the greatest explanatory power ($r^2_{adj} = 0.46$), followed by network ($r^2_{adj} = 0.38$); local, watershed, and hillslope zones had relatively low explanatory power (r^2_{adj} ranging from 0.22 to 0.34; Fig. 6). Proportion agriculture was also selected as a significant model term, with a positive relationship with EI, for all zones of influence. Intermediate watersheds had very little spread in LULC distributions for urban and agriculture (Fig. 3*a*). Explanatory power (i.e., adjusted r^2) for all zones of influence was generally lower than either the smallest or largest watersheds (Fig. 6).

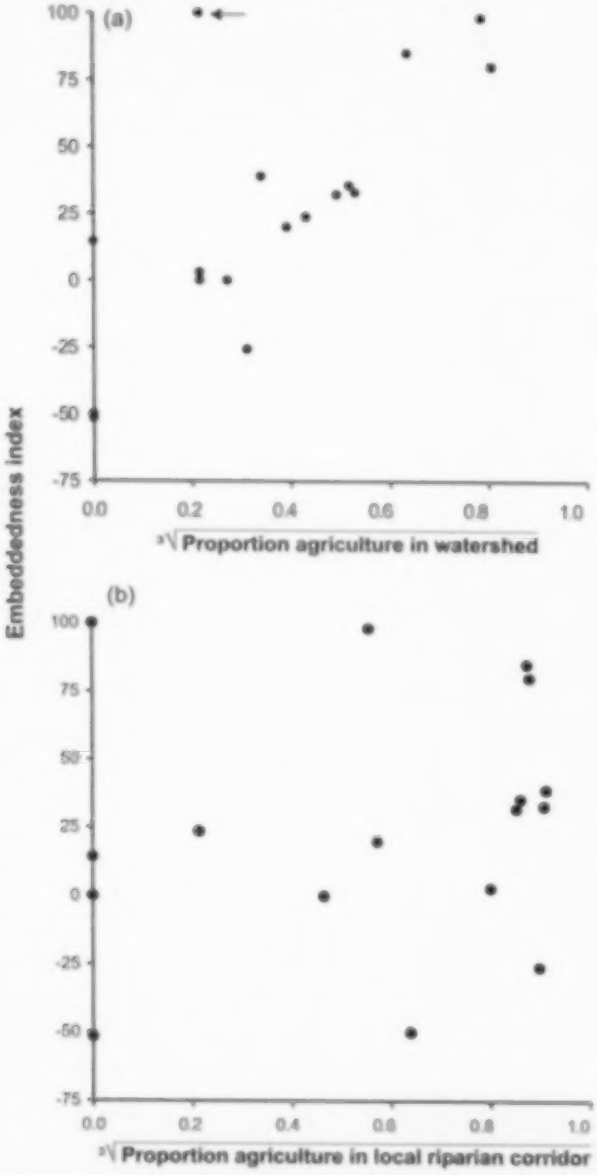
Repeating the watershed zone analyses after removing watersheds with >10% THP somewhat strengthened the explanatory power for the overall set of watersheds ($n = 39$) and the largest watersheds ($n = 14$) but did not change the explanatory power for the smallest watersheds ($n = 14$). The two methods of summarizing embeddedness from the CDFG data (the EI and the weighted average) were highly correlated (correlation coefficient = 0.97). The analyses conducted with the weighted average as the response variable had essentially identical results in terms of explanatory power, model terms, and coefficients.

Discussion

LULC variables were effective predictors of the levels of embeddedness of spawning substrate in streams within the Russian River Basin. Considering all 54 watersheds, LULC had the greatest explanatory power within the watershed, network, and hillslope zones of influence, with less explanatory power for the local and upstream zones. However, watershed size appears to have some influence on the relative strengths of these relationships. The strongest overall relationships between LULC and embeddedness were found among the largest watersheds at the watershed, network, and hillslope zones (with r^2 between 0.65 and 0.73). Conversely, among the largest watersheds, the local zone had essentially no explanatory power. The next strongest relationships between LULC and EI were found among the smallest watersheds at the network and upstream scales. The intermediate watersheds had very low levels of LULC classes generally associated with sediment production in the study region (agriculture and urban), and explanatory power for analyses

© 2005 NRC Canada

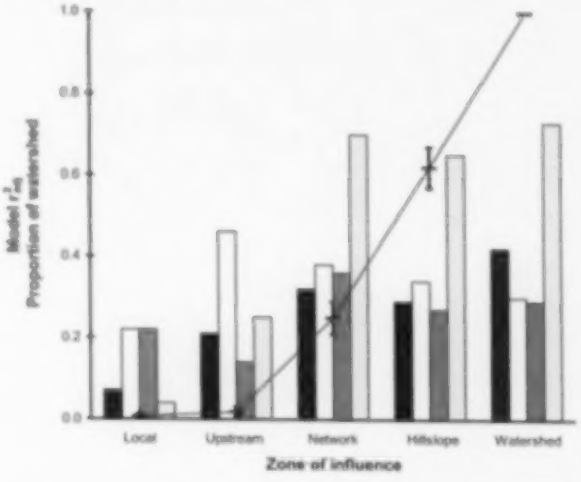
Fig. 5. (*a*) The embeddedness index plotted against the proportion of watershed in agriculture for the 18 largest watersheds; the arrow indicates a watershed that is less than 33% forested with 18% urban and the highest road density of the 54 watersheds. (*b*) The embeddedness index plotted against the proportion of the local riparian corridor in agriculture for the 18 largest watersheds. The proportion of agriculture in both zones of influence was transformed as a cube root to improve normality.



among these watersheds was generally lower than that for either the largest or smallest watersheds.

Results from our analyses showed that across multiple models and scales, LULC categories for agriculture, urban, and road density were highly significant model terms, explained the most variation in EI, and were consistently positively correlated with embeddedness, while forest cover was always negatively correlated. Agriculture can lead to significantly higher rates of sediment production, even on moderate slopes, because of the increased amount of bare soil exposed to the erosive power of raindrops and sheet wash (Dunne and Leopold 1978; Chang et al. 1982; Pimentel and Kounang 1998). Agriculture can also lead to higher rates of runoff (Chang et al. 1982), which can then increase sediment load through incision and bank erosion (Kuhnle et al. 1998). Similarly, urban land cover can increase peak runoff and, consequently, channel erosion (Trimble 1997; Pizzuto et al. 2000), in addition to the large amounts of fine sediment produced during periods of construction (Dunne and Leopold 1978). Numerous studies have linked roads with the production of sediment, particularly in areas with rugged topography (Swanson and Dyrness 1975; Montgomery 1994; Jones et al. 2000).

Fig. 6. Explanatory power (r^2_{adj}) of models focused on five zones of influence for four samples of watersheds: all 54 watersheds (solid bars), smallest (open bars), intermediate (darker shaded bars), and largest (lighter shaded bars) watersheds. The line reflects the proportion of the watershed's total area that is encompassed within a given zone of influence (median ± 25th and 75th percentiles (brackets)).



Our results suggest that increased sediment produced directly or indirectly from agricultural and urban areas and roads may be one mechanism by which these land uses degrade stream habitat and potentially influence salmonid abundance and recovery. In a study relating fish abundance with watershed characteristics, Bradford and Irvine (2000) reported that agricultural land use was associated with declines in coho salmon populations within 40 tributary watersheds of the Thompson River, British Columbia. Similarly, Pess et al. (2002) showed that coho salmon abundance in the Snohomish Basin in Washington was negatively correlated with the percentage of watershed in agriculture, urban development, and roads. The abundance of juvenile chinook salmon was also negatively correlated with road density in a study in Idaho (Thompson and Lee 2000). Sutherland et al. (2002) reported that increased fine sediment from disturbed watersheds in the southern Appalachians altered stream fish

© 2005 NRC Canada

assemblages by reducing the abundance of species that require clean gravel and cobble for spawning. Together, this research suggests that increased sediment from agriculture, urban development, and roads can alter fish abundance and assemblages.

Timber harvest is another land use frequently associated with fine-sediment delivery to streams (Everest et al. 1987; Platts et al. 1989; Lewis 1998). Although timber harvesting is less common in this region than in conifer-dominated basins of the Pacific Northwest, several watersheds in this study currently or historically contained timber harvests. However, the LULC data we used in this study could not adequately characterize the role of forestry activities (e.g., timing, type, or extent of harvests). Timber harvest may have contributed to some of the unexplained variation in the models, as the measure of r^2 generally improved after removing 14 watersheds likely affected by historical or current forestry activities.

In our analysis, different size groups of watersheds displayed different patterns of explanatory power between LULC and EI across different zones of influence. These different trends likely reflect differences in (*i*) spatial distribution of land-use type, (*ii*) spatially dependent processes, and (*iii*) data resolution. For example, the relatively low explanatory power of models for the intermediate-sized watersheds is likely due to the small amounts of urban and agricultural developments within them. Because there was so little variation in these explanatory variables, it is not surprising that LULC variables could explain relatively little variation in EI. Therefore, it is difficult to draw generalizations about watershed scale from the intermediate watersheds.

The strongest relationships overall occurred among the largest watersheds, which may be in part because these watersheds had the broadest distribution of values for explanatory variables such as urban, agriculture, and forest. However, the distributions for road density were very similar among the three size groups of watersheds, and the large watersheds had a much stronger relationship between road density and EI ($r^2 = 0.58$) than did the intermediate ($r^2 = 0.33$) and small ($r^2 = 0.04$) watersheds, suggesting that factors in addition to the distribution of explanatory variables are responsible for the differences in explanatory power based on watershed size.

Much of the difference in explanatory power between the watershed size groups is likely due to the natural tendency of smaller watersheds to have more variable sediment fluxes than large watersheds (Benda and Dunne 1997). In mountainous watersheds, landslides and other mass-wasting events, including natural events and those induced by roads, timber harvest, or other activities, are often responsible for a large proportion of the sediment supply to a channel network (Dietrich and Dunne 1978; Montgomery et al. 2000). Mass wasting is stochastic in both space and time (Kelsey 1980) and, within small watersheds, can be a rare event. Within watersheds of progressively larger drainage area (i.e., aggregating numerous small watersheds), the frequency and number of landslides within the basin increases correspondingly. Larger watersheds integrate the stochastic pulses of sediment occurring within their smaller subcatchments and thus dampen the variability of sediment fluxes through reaches that drain large areas. Because of this process of integrating sediment inputs, larger watersheds are more likely to show a land-use signal resulting from the different rates of runoff and sediment produced by different land covers (Wark and Keller 1963; Dunne and Leopold 1978; Chang et al. 1982).

Further, it is likely that small watersheds were more strongly influenced by conditions and processes that we could not detect with the resolution of our data. For example, a small watershed (e.g., <1000 ha) that is mostly forested may contain an unpaved road network throughout the watershed that is particularly problematic in terms of sediment production. It is less likely that a large watershed (e.g., 10 000 ha) that is primarily forested would encompass a similarly extensive (relative to watershed area) problematic road network. Thus, because forested areas generally produce less sediment than other land classes (Chang et al. 1982; Sutherland et al. 2002), the larger watershed will show a sediment signal more influenced by its overall land cover. Additionally, it is much more likely that a discreet land-use conversion event (such as timber harvest or clearing an oak woodland for a vineyard) will generate a more readily detectable sediment signal in a small watershed than in a large one. Because our LULC data are snapshots in time, they may be more appropriate for capturing the coarse-scale and integrative relationship between LULC and sediment in larger watersheds.

Results from our study also showed that LULC variables within several different zones of influence were good predictors of embeddedness, with variations according to watershed size. Strayer et al. (2003) hypothesized that the spatial arrangement of patches was more critical within small watersheds (<1000 ha) than it was for large watersheds. Conversely, variables that integrate information, such as proportion of a watershed in agriculture, will have greater explanatory power for large watersheds, which integrate inputs from numerous small watersheds. Consistent with this hypothesis, we found the strongest relationships between LULC and EI among the smallest watersheds were within the network and upstream zones. These zones, which are directly adjacent to the drainage network or main stem, provide more information about the spatial arrangement of patches than do the watershed or hillslope zones. Among the large watersheds, the network zone had very high explanatory power, but so did the hillslope and watershed zones.

This potential effect of scale (watershed size) on explanatory power may partly explain past conflicting results and should also be considered in any similar analysis. For example, Jones et al. (1999) and Sponseller et al. (2001) concluded that riparian land use (a scale which provides information on spatial arrangement) had stronger influence on in-stream variables than did catchment-scale land use (an integrative scale); the watersheds in these studies averaged 535 and 2366 ha, respectively. Conversely, studies by Roth et al. (1996) and Hunsaker and Levine (1995) showed that the watershed characteristics, rather than the riparian corridor characteristics, had greater influence on in-stream habitat; these watersheds averaged 6804 and 93 000 ha, respectively. Our comparative approach demonstrates that the size of the study watersheds may be one reason for differences observed between these studies.

In this study, we found that the local zone generally had minimal predictive power for embeddedness. The moderate explanatory power for the local zone among small watersheds may be due, in part, to the higher correlation between

© 2005 NRC Canada

LULC classes (e.g., forest and agriculture) at the local and watershed zones for small watersheds than for large watersheds. The general lack of influence of the local zone is not surprising, given that it represents a very small proportion of the total watershed and the surveyed reaches are receiving runoff from hundreds to thousands of hectares. Because riparian land cover had little relationship to embeddedness, it is unlikely that reach-scale riparian restoration will improve spawning conditions within the lower reaches of watersheds if conditions within the rest of the watershed remain unchanged. However, we do want to note that it is difficult to determine which zone of influence has the strongest predictive power for embeddedness, in large part because LULC in the zones of watershed, hillslope, and network are so highly correlated.

Because the LULC variables were derived from one moment in time, this analysis cannot account for the timing of land-use conversion or capture the legacies of historical land use, which can continue to exert influences on streams for decades (Harding et al. 1998). Historical legacies and the timing of conversions are undoubtedly responsible for a large portion of the unexplained variation in the models. Studies, such as this one, that examine relationships between current land-use patterns and in-stream variables must be cautious to not infer causation from correlation. For example, we do not know the distribution of embeddedness values within Russian River watersheds prior to any anthropogenic changes in land cover. However, comparing the distributions of EI within watersheds with no development with those more than 5% developed provides strong support for the role of anthropogenic land-cover conversion in increasing sediment levels in Russian River tributary streams. Although this study's approach cannot explain the mechanisms by which this happened, the mechanisms by which changes in land cover increase sediment production are well established at smaller scales (e.g., plots, small experimental watersheds) (Dunne and Leopold 1978; Chang and Tsai 1991; Battany and Grismer 2000). Combining empirical approaches with future mechanistic research (both experimental and modeling) will further improve our understanding of the linkages between land use and in-stream habitat (Strayer et al. 2003).

Our data are the first to relate patterns of fine sediments in streams to patterns of land use in Mediterranean-climate watersheds in California, and these data suggest that agricultural land use is correlated with elevated levels of fine sediment. Over the past decade, vineyards in the Russian River and Napa River basins have expanded onto hillslopes because of limited land availability in valley bottoms (Merenlender 2000). A recent study projects that 80% of future vineyards in Napa County will be planted on hillslopes (Napa County RCD 1997). Hillside vineyards in this region can produce annual soil loss ranging from 5 to 50 t·ha^{-1} (Battany and Grismer 2000). Battany and Grismer (2000), working in Napa County, found that soil cover was the primary factor affecting erosion rates from hillslope vineyards, with slope as a secondary factor. This observation emphasizes the potentially important role that management practices can play in reducing the impacts from agricultural land use.

In conclusion, the results of our study suggest that watershed-scale patterns of land use, including both the land adjacent to the entire upstream channel network and the surrounding hillslopes, are generally the best predictors of stream sediment conditions. Local land cover (i.e., the adjacent riparian corridor) had little relationship to embeddedness. Much attention and resources have been spent on piecemeal stream restoration and sediment control efforts at the local scale (e.g., bank stabilization). Our data indicate that the effects of such localized efforts will be overwhelmed by processes operating at larger scales and, thus, have little influence on spawning conditions. Rather, to improve spawning gravels, restoration efforts should emphasize protecting riparian corridors throughout entire watersheds and promote programs or policies that ameliorate the influences of roads and agricultural land use. However, even watersheds with relatively low levels of development (e.g., 5% of a watershed) had relatively high embeddedness scores, suggesting a limit to the improvements that restoration programs can hope to achieve. The landscape-scale approach of this study emphasizes the overarching importance of large-scale land-use patterns. With such an approach, managers and policy-makers can identify priority areas for protection and restoration and, when combined with projections of future land-use change, identify particularly vulnerable watersheds.

Acknowledgements

This research was funded by the University of California's Water Resources Center and the California Department of Fish and Game. We thank Robert Coey, Barry Collins, and Derek Acomb for the habitat data and continued support of our research efforts and G.M. Kondolf for input on an earlier version of this paper.

References

Allan, J.D., and Johnson, L.B. 1997. Catchment-scale analysis of aquatic ecosystems. Freshw. Biol. **37**: 107–111.

Allan, J.D., Erickson, D.L., and Fay, J. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshw. Biol. **37**: 149–161.

Battany, M.C., and Grismer, M.E. 2000. Rainfall runoff and erosion in Napa Valley vineyards: effects of slope, cover and surface roughness. Hydrol. Process. **14**: 1289–1304.

Benda, L., and Dunne, T. 1997. Stochastic forcing of sediment supply to channel networks from landsliding and debris flows. Water Resour. Res. **33**: 2849–2863.

Bradford, M.J., and Irvine, J.R. 2000. Land use, fishing, climate change, and the decline of Thompson River, British Columbia, coho salmon. Can. J. Fish. Aquat. Sci. **57**: 13–16.

Busby, P.J., Wainwright, T.C., and Bryant, G.J. 2000. Status review of steelhead from Washington, Idaho, Oregon, and California. *In* Sustainable fisheries management: Pacific salmon. *Edited by* E.E. Knudsen, C.R. Steward, D.D. MacDonal, J.E. Williams, and D.W. Reiser. Lewis Publishers, Nev. York. pp. 119–132.

Chang, K., and Tsai, B. 1991. The effect of DEM resolution on slope and aspect mapping. Cartogr. Geogr. Inform. **18**: 69–77.

Chang, M., Roth, F.A., and Hunt, E.V. 1982. Sediment production under various forest-site conditions. *In* Recent developments in the explanation and prediction of erosion and sediment yield. Int. Assoc. Hydrol. Sci. Publ. No. 137, Wallingford, UK. pp. 13–22.

© 2005 NRC Canada

Dietrich, W.E., and Dunne, T. 1978. Sediment budget for a small catchment in mountainous terrain. Z. Geomorphol. **29**(Suppl.): 191–206.

Dunne, T., and Leopold, L.B. 1978. Water in environmental planning. W.H. Freeman and Company, New York.

Everest, F.H., Beschta, R.L., Scrivener, J.C., Koski, K.V., Sedell, J.R., and Cederholm, C.J. 1987. Fine sediment and salmonid production: a paradox. *In* Streamside management: forestry and fisheries interactions. *Edited by* E.O. Salo and T.W. Cundy. University of Washington Press, Seattle, Wash. pp. 98–142.

Gasith, A., and Resh, V.H. 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. Annu. Rev. Ecol. Syst. **30**: 51–81.

Hansen, W.F. 2001. Identifying stream types and management implications. For. Ecol. Manag. **143**: 39–46.

Harding, J.S., Benfield, E.F., Bolstad, P.V., Helfman, G.S., and Jones, E.B.D.I. 1998. Stream biodiversity: the ghost of land use past. Proc. Natl. Acad. Sci. U.S.A. **95**: 14 843–14 847.

Heaton, E., and Merenlender, A.M. 2000. Modeling vineyard expansion, potential habitat fragmentation. Calif. Agric. **54**: 12–19.

Henley, W.F., Patterson, M.A., Neves, R.J., and Lemly, A.D. 2000. Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. Rev. Fish. Sci. **8**: 125–139.

Hunsaker, C.T., and Levine, D.A. 1995. Hierarchical approaches to the study of water quality in rivers. Bioscience, **45**: 193–203.

Jones, E.B.D.I., Helfman, G.S., Harper, J.O., and Bolstad, P.V. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conserv. Biol. **13**: 1454–1465.

Jones, J.A., Swanson, F.J., Wemple, B.C., and Snyder, K.U. 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. Conserv. Biol. **14**: 76–85.

Kelsey, H.M. 1980. A sediment budget and an analysis of geomorphic process in the Van Duzen River basin, north coastal California. Geol. Soc. Am. Bull. **91**: 190–195.

Kondolf, G.M. 2000. Assessing salmonid spawning gravel quality. Trans. Am. Fish. Soc. **129**: 262–281.

Kuhnle, R.A., Bingner, R.L., Foster, G.R., and Grissinger, E.H. 1998. Land use change and sediment transport in Goodwin Creek. *In* Gravel-bed rivers in the environment. *Edited by* P.C. Klingeman, R.L. Beschta, P.D. Komar, and J.B. Bradley. Water Resources Publications, LLC, Highlands Ranch, Co. pp. 279–292.

Lammert, M., and Allan, J.D. 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environ. Manag. **23**: 257–270.

Lewis, J. 1998. Evaluating the impacts of logging activities on erosion and suspended sediment transport in the Caspar Creek watersheds. *In* Proceedings of the conference on coastal watersheds: the Caspar Creek story. *Edited by* R.R. Ziemer. Pacific Southwest Research Station, Forest Service, US Department of Agriculture, Ukiah, Calif. pp. 55–69.

McIntosh, B.A., Sedell, J.R., Thurow, R.F., Clarke, S.E., and Chandler, G.L. 2000. Historical changes in pool habitats in the Columbia River Basin. Ecol. Appl. **10**: 1478–1496.

Merenlender, A.M. 2000. Mapping vineyard expansion provides information on agriculture and the environment. Calif. Agric. **54**: 7–12.

Merenlender, A.M., Heise, K.L., and Brooks, C. 1998. Effects of subdividing private property on biodiversity in California's north coast oak woodlands. Trans. W. Sect. Wild. Soc. **34**: 9–20.

Mills, T.J., McEwan, D., and Jennings, M.R. 1997. California salmon and steelhead: beyond the crossroads. *In* Pacific salmon and their ecosystems: status and future options. *Edited by* D.J. Stouder, P.A. Bisson, R.J. Naiman, and M.G. Duke. Chapman & Hall, New York. pp. 91–112.

Montgomery, D.R. 1994. Road surface drainage, channel initiation, and slope instability. Water Resour. Res. **30**: 1925–1932.

Montgomery, D.R., and Buffington, J.M. 1993. Channel classification, prediction of channel response, and assessment of channel condition. Washington Department of Natural Resources Rep. No. TFW-SH10-93-002.

Montgomery, D.R., and Dietrich, W.E. 1988. Where do channels begin? Nature (Lond.), **336**: 232–234.

Montgomery, D.R., Schmidt, K.M., Greenberg, H.M., and Dietrich, W.E. 2000. Forest clearing and regional landsliding. Geology, **28**: 311–314.

Moyle, P.B. 2002. Inland fishes of California. University of California Press, Berkeley, Calif.

Napa County Resource Conservation District (RCD). 1997. Napa River watershed owner's manual. Napa County Resource Conservation District, Napa, Calif.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Nehlsen, W. 1997. Pacific salmon status and trends — a coastwide perspective. *In* Pacific salmon and their ecosystems: status and future options. *Edited by* D.J. Stouder, P.A. Bisson, R.J. Naiman, and M.G. Duke. Chapman & Hall, New York. pp. 41–52.

Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk in California, Oregon, Idaho and Washington. Fisheries, **16**: 4–21.

Nilsson, C., Pizzuto, J.E., Moglen, G.E., Palmer, M.A., Stanley, E.H., Bockstael, N.E., and Thompson, L.C. 2003. Ecological forecasting and the urbanization of stream ecosystems: challenges for economists, hydrologists, geomorphologists, and ecologists. Ecosystems, **6**: 659–674.

Omernik, J.M., Abernathy, A.R., and Male, L.M. 1981. Stream nutrient levels and proximity of agricultural and forest land to streams: some relationships. J. Soil Water Conserv. **36**: 227–231.

Paulsen, C.M., and Fisher, T.R. 2001. Statistical relationship between parr-to-smolt survival of Snake River spring–summer Chinook salmon and indices of land use. Trans. Am. Fish. Soc. **130**: 347–358.

Pess, G.R., Montgomery, D.R., Steel, E.A., Bilby, R.E., Feist, B.E., and Greenberg, H.M. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Wash., U.S.A. Can. J. Fish. Aquat. Sci. **59**: 613–623.

Pimentel, D., and Kounang, N. 1998. Ecology of soil erosion in ecosystems. Ecosystems, **1**: 416–426.

Pizzuto, J.E., Hession, W.C., and McBride, M. 2000. Comparing gravel-bed rivers in paired urban and rural catchments of southeastern Pennsylvania. Geology, **28**: 79–82.

Platts, W.S., Torquemada, R.J., McHenry, M.L., and Graham, C.K. 1989. Changes in salmonid spawning and rearing habitat from increased delivery of fine sediment to the South Fork Salmon River, Idaho. Trans. Am. Fish. Soc. **118**: 274–283.

Radko, M.A. 1997. Spatially linking basinwide stream inventories to arcs representing streams in a Geographic Information System. USDA Forest Service Rep. INT-GTR-345.

Regetz, J. 2003. Landscape-level constraints on recruitment of chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River Basin, U.S.A. Aquat. Conserv. **13**: 35–49.

Reiser, D.W., and White, R.G. 1988. Effects of two sediment size-classes on survival of steelhead and chinook salmon eggs. N. Am. J. Fish. Manag. **8**: 432 – 437.

Richards, C., Johnson, L.B., and Host, G.E. 1996. Landscape-scale influences on stream habitats and biota. Can. J. Fish. Aquat. Sci. **53**: 295–311.

© 2005 NRC Canada

Roni, P., Beechie, T.J., Bilby, R.E., Leonetti, F.E., Pollock, M.M., and Pess, G.R. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. N. Am. J. Fish. Manag. **22**: 1–20.

Roper, B.D., Dose, J.J., and Williams, J.E. 1997. Stream restoration: is fisheries biology enough? Fisheries, **22**: 6–11.

Roth, N.E., Allan, J.D., and Erickson, D.L. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landsc. Ecol. **11**: 141–156.

Snyder, C.D., Young, J.A., Villella, R., and Lemarie, D.P. 2003. Influences of upland and riparian land use patterns on stream biotic integrity. Landsc. Ecol. **18**: 647–664.

Sponseller, R.A., Benfield, E.F., and Valett, H.M. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. Freshw. Biol. **46**: 1409–1424.

Strayer, D.L., Beighley, R.E., Thompson, L.C., Brooks, S., Nilsson, C., Pinay, G., and Naiman, R.J. 2003. Effects of land-cover on stream ecosystems: roles of empirical models and scaling issues. Ecosystems, **6**: 407–423.

Sutherland, A.B., Meyer, J.L., and Gardiner, E.P. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. Freshw. Biol. **47**: 1791–1805.

Suttle, K.B., Power, M.E., Levine, J.M., and McNeely, C. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecol. Appl. **14**: 2004.

Swanson, F.J., and Dyrness, C.T. 1975. Impact of clear-cutting and road construction on soil erosion by landslides in the western Cascade Range, Oregon. Geology, **3**: 393–396.

Thompson, W.L., and Lee, D.C. 2000. Modeling relationships between landscape-level attributes and snorkel counts of chinook salmon and steelhead parr in Idaho. Can. J. Fish. Aquat. Sci. **57**: 1834–1842.

Trimble, S.W. 1997. Contribution of stream channel erosion to sediment yield from an urbanizing watershed. Science (Wash., D.C.), **278**: 1442–1444.

Wang, L., Lyons, J., Kanehl, P., and Gatti, R. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries, **22**: 6–12.

Wark, J.W., and Keller, F.J. 1963. Preliminary study of sediment sources and transport in the Potomac River Basin. Interstate Commission on the Potomac River Basin, Edgewater, Md.

Waters, T.F. 1995. Sediment in streams: sources, biological effects and control. Am. Fish. Soc. Monogr. No. 7, Bethesda, Md.

Weitkamp, L., Wainwright, T.C., Bryant, G.J., Teel, D.J., and Kope, R.G. 2000. Review of the status of coho salmon from Washington, Oregon, and California. *In* Sustainable fisheries management: Pacific salmon. *Edited by* E.E. Knudsen, C.R. Steward, D.D. MacDonal, J.E. Williams, and D.W. Reiser. Lewis Publishers, New York. pp. 111–118.

Wohl, N.E., and Carline, R.F. 1996. Relations among riparian grazing, sediment loads, macroinvertebrates, and fishes in three central Pennsylvania streams. Can. J. Fish. Aquat. Sci. **53**(Suppl. 1): 260–266.

© 2005 NRC Canada

Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus* spp.

Kentaro Morita, Shoko H. Morita, Masa-aki Fukuwaka, and Hiroyuki Matsuda

Abstract: In the last quarter of the 20th century, the size at maturity of many North Pacific salmon (*Oncorhynchus* spp.) populations decreased. During this same period, the age at maturity increased, implying that the growth rate of Pacific salmon decreased, probably owing to environmental changes. To elucidate these trends, we identified the rule of age and size at maturity of Japanese chum salmon (*Oncorhynchus keta*), which was that slow-growing salmon initiated maturation at an older age and smaller size than did fast-growing salmon. We then simulated the potential modification of age and size at maturity in response to changing growth rate using a size-structured model with age- and size-specific maturation rates. This showed that reducing the growth rate without assuming a genetic change was sufficient for realistic modeling of recent changes. In addition, the observed rule of age and size at maturity was consistent with the optimal age and size at maturity in terms of maximizing the fitness. Our results attributed the recent trends in chum salmon's increasing age and decreasing size at maturity to an adaptive phenotypic response to a reduced growth rate.

Résumé : Durant le dernier quart du 20e siècle, la taille à la maturité a décliné chez plusieurs populations de saumons (*Oncorhynchus* spp.) du Pacifique Nord. Durant la même période, l'âge à la maturité a augmenté, ce qui indique que le taux de croissance des saumons du Pacifique a diminué, probablement à cause des changements environnementaux. Afin d'élucider ces tendances, nous avons identifié la règle de la taille et de l'âge à la maturité du saumon kéta (*Oncorhynchus keta*) du Japon, qui veut que les saumons à croissance lente commencent leur maturation à un âge plus avancé et à une taille plus petite que les saumons à croissance rapide. Nous avons ensuite simulé une modification potentielle de l'âge et de la taille à la maturité en réaction à des changements de taux de croissance, à l'aide d'un modèle structuré en fonction de la taille possédant des taux de maturation spécifiques à l'âge et à la taille. Cette simulation démontre qu'une réduction du taux de croissance, sans présupposition de changement génétique, suffit pour permettre de modéliser de façon réaliste les changements récents. De plus, la règle de l'âge et de la taille à la maturité observée est compatible avec l'âge et la taille à la maturité optimaux de façon à maximiser le fitness. Nos résultats expliquent les tendances d'augmentation de l'âge et de diminution de la taille à la maturité chez le saumon kéta par une réaction phénotypique à une réduction du taux de croissance.

[Traduit par la Rédaction]

Introduction

In the last quarter of the 20th century, the size at maturity of North Pacific salmon (*Oncorhynchus* spp.) decreased dramatically (reviewed by Bigler et al. 1996). During this same period, however, the age at maturity increased. These trends are particularly pronounced in chum salmon (*Oncorhynchus keta*) over the range of its distribution, including North America (Helle and Hoffman 1995), Russia (Kaev 2000), and Japan (Kaeriyama 1998). For example, the average age at maturity of chum salmon returning to Hokkaido, Japan, increased from 3.7 years before 1972 to over 4.0 years after 1980, but the average size at maturity at age 4 years decreased from 68.7 cm in the 1970s to 63.8 cm in the 1980s (Kaeriyama 1998).

Selection generated by fishing has long been suggested as being a contributory factor to changing age and size at maturity of commercial fish (reviewed by Trippel 1995; Law 2000). If age and size at maturity are heritable traits, selection for early maturation at a smaller size will occur with exploitation (Trippel 1995; Law 2000). In fact, the age and size at maturity of heavily exploited fish stocks decreased

Received 27 December 2004. Accepted 29 June 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 2 November 2005.
J18478

K. Morita[1] **and S.H. Morita.** Hokkaido National Fisheries Research Institute, Fisheries Research Agency, 116 Katsurakoi, Kushiro 085-0802, Japan.
M. Fukuwaka.[2] National Salmon Resources Center, 2-2 Nakanoshima, Toyohira-ku, Sapporo 062-0922, Japan.
H. Matsuda. Graduate School of Environment and Information Sciences, Yokohama National University, Hodogaya-ku, Yokohama 240-8501, Japan.

[1]Corresponding author (e-mail: moritak@affrc.go.jp).
[2]Present address: Hokkaido National Fisheries Research Institute, Fisheries Research Agency, 116 Katsurakoi, Kushiro 085-0802, Japan.

 doi: 10.1139/f05-182 © 2005 NRC Canada

dramatically in the 20th century (e.g., Rijnsdorp 1993; Rowell 1993; Haugen and Vøllestad 2001). Similarly, Ricker (1981, 1995) has argued that a reduced frequency of fast-growth genes, owing to size-selective fishing, is largely responsible for the decrease in size at maturity of Pacific salmon. However, the age at maturity of indeterminate semelparous species, such as chum salmon, sockeye salmon (*Oncorhynchus nerka*), and chinook salmon (*Oncorhynchus tshawytscha*), has tended to increase (Bigler et al. 1996). Although size-selective fishing can explain decreasing size at maturity, it is difficult to explain increasing age at maturity, as has been pointed out by Healey (1986).

Environmental changes have also been suggested as contributing to the changing age and size at maturity of Pacific salmon (chum salmon: Ishida et al. 1993, 1995; Morita et al. 2001; sockeye salmon: Hinch et al. 1995; Cox and Hinch 1997; Pyper and Peterman 1999). Ishida et al. (1993, 1995) found that increases in abundance and decreases in sea surface temperature were significantly associated with reduced body length for North Pacific chum salmon. In addition, Morita et al. (2001) found that a decrease in sea surface salinity, which is probably related to global warming, was significantly associated with the reduced growth rate of chum salmon in the Sub-Arctic Domain of the Western North Pacific. Pyper and Peterman (1999) found that increases in abundance and sea surface temperature were significantly associated with reduced body length for British Columbia and Alaska sockeye salmon. While a recent increase in salmon abundance might be associated with improved ocean productivity (Beamish et al. 1999), if the increased salmon abundance exceeds the improved ocean productivity, it would lead to increased competition and decreased food availability.

As mentioned above, many studies have provided strong evidence showing that environmental changes have caused a reduction in the growth rate of Pacific salmon. However, there have been few efforts thus far to devise a comprehensive model that connects age at maturity, size at maturity, and the reduced growth rate of Pacific salmon. To clarify the causes of the recent trends in age and size at maturity, it is first necessary to identify the rule of age and size at maturity, and then it should be possible to quantify how age and size at maturity change in response to a changing growth rate. The objectives of this study were (*i*) to identify the rules governing the age and size at maturity of Japanese chum salmon, (*ii*) to elucidate the ecological significance of the observed rules for age and size at maturity, and (*iii*) to examine whether the recent trend in age and size at maturity can be explained by a phenotypic plasticity to a reduction in growth rate (i.e., an environmental response).

Data

We obtained data on chum salmon ascending the Shari River (43°55′N, 144°40′E), eastern Hokkaido, Japan, during the breeding season of 1992–1997. The data include fork length, sex, and age determined by scale of individuals (n = 684–1168 for each year) and the number of fish captured at the weir for each sex. Because nearly all chum salmon (99.97%) matured by age 6, the data cover three cohorts, the 1989, 1990, and 1991 brood years. In this study, we used these three cohorts for the analyses.

To reconstruct the fork length of immature fish, we estimated the past fork lengths at each age using a back-calculation method based on scale length and annulus length measurements using a biological intercept method (Campana 1990):

$$(1) \qquad l_t = l_c + \frac{S_t - S_c}{S_c - S_0}(l_c - l_0)$$

where l_t is the back-calculated fork length at age t, S_t is the annulus length at t, S_c is the total scale length, l_c is the fork length at the time of capture, and l_0 and S_0 are the fork length and scale length at the time of scale formation. For this species, l_0 = 4.0 cm and S_0 = 0.114 mm (Fukuwaka and Kaeriyama 1994). We assumed that annuli form in winter and little or no growth occurs during winter (Salo 1991). So, the back-calculated size could correspond to the size of immature fish at the breeding season (i.e., during October and December). The back-calculation was performed on 100 fish by year of sampling and return age, if available (n = 241–378 for each year of sampling).

To calculate the probability of maturing, we estimated age and size frequency distribution of immature and mature fish for each sex. The number of maturing fish of size class i at age t, denoted by $n_{i,t}$, was described by

$$(2) \qquad n_{i,t} = C \times f_t \times p_i$$

where C is the number of fish captured at the weir (a surrogate for population size) and f_t and p_i are observed age and size probability distributions, respectively. The number of immature fish of size class i at age $t - a$ that mature at age t, denoted by $n_{i,t-a}$, was described by

$$(3) \qquad n_{i,t-a} = \sum_i n_{i,t} \times e^{Ma} \times q_{i,t-a,t}$$

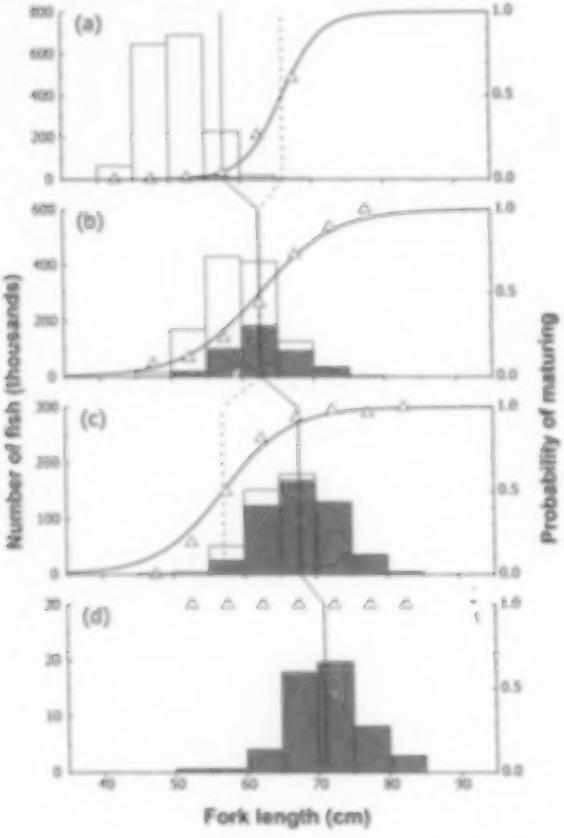
where M is the instantaneous mortality rate and $q_{i,t-a,t}$ is the back-calculated size probability distribution at age $t - a$ from fish mature at age t. The method described above resembles virtual population analysis in following a cohort backwards in time (cf. Heino et al. 2002*a*).

The baseline mortality was set at M = 0.314, which is the average of three previous studies (Parker 1962; Ricker 1964; Watanabe 1999). Parker (1962) estimated the ocean mortality of Pacific salmon at M = 0.316 from broad empirical data. Ricker (1964) suggested that 0.02·month^{-1} (i.e., M = 0.24) is a reasonable value for the ocean mortality for salmon 30 cm long and longer. Watanabe (1999) estimated the natural mortality of Japanese chum salmon in oceanic waters at M = 0.357 and 0.417 for different regions using the empirical equation of Tanaka (1960). Consequently, the estimated M includes uncertainty. Therefore, we also used M = 0.2 and 0.5 to cover the possible range of mortality.

In addition, we collected a published database to quantify the changes in average age and size at maturity during the last few decades in Hokkaido. The Hokkaido Salmon Hatchery (1956, 1959) and National Salmon Resources Center (2000*a*, 2000*b*, 2002) reported the age and fork length composition of chum salmon migrating into the major streams in Hokkaido during the periods 1950–1957 and 1998–2000, respectively. The averages of each database were used as rep-

© 2005 NRC Canada

Fig. 1. Fork length distribution at each age of chum salmon (*Oncorhynchus keta*): open bars, immature; shaded bars, mature. Probability of maturing plotted on fork length: thick lines, estimated logistic regressions; triangles, observed probability of maturing at each size class. Thin lines represent the average size at maturity. Broken lines represent 50% size at maturity. (*a*) age 3; (*b*) age 4; (*c*) age 5; (*d*) age 6.



resentative of the past and present age and size at maturity of chum salmon.

Observed age and size at maturity

Chum salmon ascending the Shari River showed individual variability in age and size at maturity. The age at maturity varied from 3 to 7 years (n = 3414), although only one fish matured at age 7 years. The size at maturity varied from 45 to 84 cm in fork length (n = 3414).

To examine the rule of age and size at maturity, it is necessary to clarify the threshold, which is defined as the size at which 50% of the individuals are mature (Metcalf et al. 2003). Therefore, logistic regression analysis is appropriate (Heino et al. 2002*b*; Morita and Morita 2002). The form of the logistic function is

$$(4) \quad \text{logit}(P) = \log\left(\frac{P}{1-P}\right) = c_0 + c_1 l + c_{2,s} + c_{3,s} + c_{4,b}$$

Table 1. Estimated threshold (50% probability of maturing) size at maturity ± SD of chum salmon (*Oncorhynchus keta*) at each age for different mortality assumptions.

	Age 3	Age 4	Age 5
M = 0.2	65.7±5.0	61.8±9.8	56.5±8.6
M = 0.314	66.0±5.0	62.5±9.6	57.1±8.6
M = 0.5	66.5±4.9	63.7±9.4	58.0±8.6

where P is the probability of maturing, c_0 is constant, c_1 is the coefficient for l (fork length), and c_2, c_3, and c_4 are constant for each t (age), s (sex), and b (brood year) group, respectively. Although several logistic models have been suggested for reaction norms of age and size at maturity (Heino et al. 2002*b*), we used the simplest model (eq. 4 corresponds to eq. A5 of Heino et al. 2002*b*). We analyzed the probability of maturing per 5-cm size class.

Logistic regression analysis identified significant effects of age and fork length on the probability of maturing (fork length: $F_{[1,61]}$ = 152.4, $p < 0.001$; age: $F_{[2,61]}$ = 76.4, $p < 0.001$; sex: $F_{[1,61]}$ = 0.553, p = 0.460; brood year: $F_{[2,61]}$ = 1.67, p = 0.197). The probability of maturing increased with fork length, but the threshold (50% probability of maturing) size at maturity decreased with increasing age (Fig. 1). Therefore, the relationship between threshold size and age at maturity was negative. Note that the average size at maturity increased with age, but this does not mean that older fish need a larger body size to mature. These results indicate that slow-growing fish initiate maturation at an older age and smaller size but mature at an older age and larger size than do fast-growing fish.

The results of logistic regression were robust to assumptions regarding mortality. The estimated threshold (50% probability of maturing) size at maturity was a little sensitive to changes in mortality (Table 1).

Optimal age and size at maturity

Age and size at maturity are two of the most important life history traits affecting the fitness of fish (Roff 1984; Mangel 1996). Early maturation increases the probability of survival to reproduction. By contrast, delayed maturation increases body size, which in turn increases fecundity. Therefore, there is a trade-off between the probability of survival to reproduction and fecundity. Several studies have shown that optimal solutions to maximize fitness under the trade-off explain the inter- and intra-specific variation in age and size at maturity (e.g., among marine fishes: Roff 1984; brook trout (*Salvelinus fontinalis*): Hutchings 1993; brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*): Mangel 1996).

To quantify the optimal rule of age and size at maturity of chum salmon, we used the Roff (1984) general life history model for fish. The fish length at age t is described using the simplified von Bertalanffy growth equation:

$$(5) \quad l_t = l_\infty(1 - e^{-kt})$$

where l_t is the length at age t, l_∞ is the asymptotic length, and k is the rate of growth towards the asymptotic length. The asymptotic length was set at l_∞ = 85 cm, which is near

© 2005 NRC Canada

the maximum fork length observed in chum salmon. Generally, weight is proportional to length cubed and fecundity is proportional to weight. The net reproductive rate R_0 can be approximated by

$$(6) \qquad R_0 = A e^{-Mt}[l_\infty(1 - e^{-kt})]^3$$

where A is the probability of surviving during early life (i.e., fresh water and coastal) and M is the instantaneous ocean mortality. Although the intrinsic rate of increase r is a general measure of fitness, selection also acts to maximize the net reproductive rate R_0 when the global population is stationary (Charnov 1990; Berrigan and Koella 1994). If we assume that the net reproductive rate R_0 is a measure of fitness, the optimal age at maturity t^* maximizing fitness can be determined analytically by setting $\partial R_0/\partial t = 0$, yielding

$$(7) \qquad t^* = \frac{1}{k}\ln\left(\frac{3k + M}{M}\right)$$

The optimal size at maturity l^* can be determined by substituting t^* into eq. 5, yielding

$$(8) \qquad l^* = l_\infty\left(\frac{3k}{3k + M}\right)$$

In this model, the optimal solution is independent of A, the probability of surviving during early life, where density-dependent regulation occurs for anadromous salmonids (Elliott 1993; Fukushima et al. 1998; Fukuwaka and Suzuki 2000). Therefore, the optimal solution could include the assumption that the global population is stationary, $r = 0$ or $R_0 = 1$; hence, the optimal solution was considered an evolutionarily stable strategy (cf. Charnov 1990; Mylius and Diekmann 1995).

We predicted the optimal rule of age and size at maturity of chum salmon for different growth rates k (Fig. 2). The predictions of the model were straightforward: slow-growing fish should initiate maturation at an older age and a smaller size than fast-growing fish. Although the predicted values were quite sensitive to changes in mortality rate, the fit between the predicted and observed rules of age and size at maturity was good enough to be encouraging. These results suggest that chum salmon exhibited adaptive phenotypic plasticity in age and size at maturity to maximize fitness, depending on individual growth conditions.

Response to changing growth: a simulation experiment

Both the empirical and the theoretical results showed that the threshold size at maturity decreased with age; however, the observed average size at maturity increased with age (i.e., slow-growing fish initiate maturation at an older age and smaller size but mature at an older age and larger size than fast-growing fish). We are interested in how average age and size at maturity change in response to changing growth rate at the population level. Here, we simulated the potential modification of average age and size at maturity in response to changing growth rate.

We constructed a size-structured model to simulate the age and size distribution of maturing fish (i.e., returning salmon). The number of maturing fish of size class i at age t, denoted by $R_{i,t}$, can be written in matrix form as

$$(9) \qquad \begin{bmatrix} R_{1,t} \\ R_{2,t} \\ \vdots \\ R_{i,t} \\ \vdots \\ R_{i_\infty,t} \end{bmatrix} = \begin{bmatrix} P_{1,t} & 0 & & & & 0 \\ 0 & P_{2,t} & & & & \\ & & \ddots & & & \\ & & & P_{i,t} & & \\ & & & & \ddots & 0 \\ 0 & & & & 0 & P_{i_\infty,t} \end{bmatrix} \times \begin{bmatrix} N_{1,t} \\ N_{2,t} \\ \vdots \\ N_{i,t} \\ \vdots \\ N_{i_\infty,t} \end{bmatrix}$$

or

$$\mathbf{R}_t = \mathbf{P}\mathbf{N}_t$$

where $N_{i,t}$ is the number of fish of size class i at age t, $P_{i,t}$ is the age t and size class i specific probability of maturing according to the logistic regression, and i_∞ is the maximum size class. The number of fish of size class i at the next age, $t + 1$, denoted by $N_{i,t+1}$, can be written in matrix form as

$$(10) \qquad \begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ \vdots \\ N_{i,t+1} \\ \vdots \\ N_{i_\infty,t+1} \end{bmatrix} = e^{-M} \times \begin{bmatrix} G_{1,1} & 0 & & & & 0 \\ G_{1,2} & G_{2,2} & & & & \\ & & \ddots & & & \\ G_{1,i} & & & G_{i,i} & & \\ & & & & \ddots & 0 \\ G_{1,i_\infty} & G_{2,i_\infty} & \cdots & G_{i,i_\infty} & \cdots & G_{i_\infty,i_\infty} \end{bmatrix} \times \begin{bmatrix} N_{1,t} - R_{1,t} \\ N_{2,t} - R_{2,t} \\ \vdots \\ N_{i,t} - R_{i,t} \\ \vdots \\ N_{i_\infty,t} - R_{i_\infty,t} \end{bmatrix}$$

or

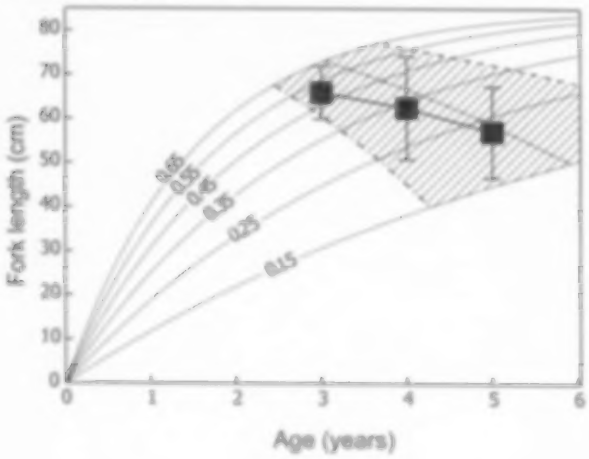
$$\mathbf{N}_{t+1} = e^{-M}\mathbf{G}(\mathbf{N}_t - \mathbf{R}_t)$$

where M is the instantaneous ocean mortality and $G_{i,j}$ is the transition probability that an individual of size class i will grow to size class j in the next year.

In the simulation, we set the minimum size at 30 cm and the maximum size at 85 cm. Fifty-five size classes were de-

© 2005 NRC Canada

Fig. 2. Growth trajectories and optimal maturation timings of chum salmon (*Oncorhynchus keta*) with different growth rates: k = 0.15, 0.25, 0.35, 0.45, 0.55, and 0.65. The hatched area represents optimal age and size at maturity in terms of maximizing fitness when the mortality rates ranged from 0.2 (dashed line) to 0.314 (dotted line) to 0.5 (dash-dotted line). Squares represent the observed threshold (50% probability of maturing) size at maturity at each age. Error bars represent ranges of 10% and 90% probability of maturing.



fined with a size-class interval of 1 cm. The size class from l_1 to l_2 cm is approximated by the midlength $l = (l_1 + l_2)/2$, e.g., the size class from 30 to 31 is approximated using 30.5. The age at first maturity was set at 3 years. The age at last maturity was set at 6 years. The initial size distribution was made from a normal distribution, with average = $85 \times (1 - e^{-k \times 3})$ and SD = 3.77 (observed value). The age t and size l specific probability of maturing was set at logit(P) = $0.365 \times l - 24.1$ for age 3, $0.188 \times l - 11.8$ for age 4, and $0.212 \times l - 12.1$ for age 5, which are estimated logistic equations as in Fig. 1. The transition probability G was obtained using a stochastic von Bertalanffy growth model (Appendix A).

The simulation experiments generated the average age and size at maturity for different growth rates, k = 0.30, 0.35, 0.40, 0.45, and 0.50 (Table 2). Decreasing k led to a decrease in the average size at maturity at each age and increase in the average age at maturity. The average size at maturity was independent of M, and the average age at maturity was a little sensitive to changes in M. The average age and size at maturity for k = 0.35 and 0.45 were comparable with present (1998–2000) and past (1950–1957) observed values, respectively. A decrease in the growth rate k from 0.45 to 0.35 corresponded to a decrease in fork length of ~5 cm at each age and an increased average age at maturity from 3.71 to 4.30 years. Therefore, the simulation experiments produced realistic changes with decreasing size at maturity and increasing age at maturity. In addition, these changes are comparable with the recent trends in Pacific salmon (Bigler et al. 1996). Our simulation results showed that recent trends in average age and size at maturity could be due to phenotypic plasticity in response to a reduced growth rate, without the occurrence of genetic change.

Discussion

The age and size at maturity of chum salmon varied among individuals. The rule of age and size at maturity held that slow-growing salmon initiated maturation at an older age and smaller size than did fast-growing salmon. This may be counterintuitive because slow-growing salmon mature at an older age and larger size than do fast-growing salmon, on average. The observed rule of age and size at maturity was consistent with the optimal age and size at maturity in terms of maximizing the net reproductive rate R_0. The simulation experiment incorporating the observed rule of age and size at maturity produced realistic changes in the age and size at maturity of chum salmon during the last quarter of the 20th century.

The negative relationship between threshold size and age at maturity observed here has been reported for a variety of fishes, e.g., North Sea plaice (*Pleuronectes platessa*) (Rijnsdorp 1993; Grift et al. 2003), grayling (*Thymallus thymallus*) (Haugen 2000), whitespotted char (*Salvelinus leucomaenis*) (Morita and Morita 2002), Atlantic cod (*Gadus morhua*) (Olsen et al. 2004; but see Heino et al. 2002*a*; Barot et al. 2004), and American plaice (*Hippoglossoides platessoides*) (Barot et al. 2005). Stearns (1983) argued that this pattern showed adaptive phenotypic plasticity. Maturation at a specific size is a risky evolutionary strategy, as fish must wait a long time under slow-growth conditions, which increases mortality before maturation. Maturation at a specific age is a costly evolutionary strategy, as fish must mature at a small size under slow-growth conditions, which decreases fecundity. Therefore, Stearns (1983) deduced that fish would adopt an intermediate rule as a compromise between mortality risk and fecundity cost (i.e., slow-growing individuals should initiate maturation at an older age and smaller size than fast-growing individuals).

An important finding of this study was that the recent decrease in size at maturity and increase in age at maturity of Japanese chum salmon could result from a reduced growth rate alone, without genetic change necessarily taking place. During the last quarter of the 20th century, the size at maturity of many populations of North Pacific salmon decreased, while the age at maturity increased (reviewed in Bigler et al. 1996). A similar life history change has been reported in kokanee (Grover 2005). In this study, we have demonstrated that such life history changes could result from a reduced growth rate. Many studies have reported a trend to decreased salmon growth and consistent relationships with environmental factors, including sea surface temperature, salinity, and population density (e.g., Ishida et al. 1993; Pyper and Peterman 1999; Morita et al. 2001). Therefore, it is plausible that salmon have exhibited adaptive phenotypic plasticity to diminish the effect of reduced growth rate by changing their life history; hence, decreasing size at maturity and increasing age at maturity would occur.

Changes in ocean mortality could affect the optimal age and size at maturity. Unfortunately, few studies have examined the oceanic mortality of chum salmon (Parker 1962; Ricker 1964; Watanabe 1999). The oceanic mortality probably changed over the last quarter of the 20th century, but this trend would differ between regions. The return rate of Japa-

© 2005 NRC Canada

Table 2. Simulated and observed average age and size at maturity of chum salmon (*Oncorhynchus keta*) at Hokkaido Island, Japan.

Population	Average size at maturity (cm)				Average age at maturity (years)		
	Age 3	Age 4	Age 5	Age 6	$M = 0.314$	$M = 0.2$	$M = 0.5$
Simulated							
$k = 0.30$	55.4	61.2	65.9	68.3	4.59	4.64	4.52
$k = 0.35$	59.7	65.1	69.4	71.7	4.30	4.34	4.23
$k = 0.40$	63.0	68.2	72.2	74.4	4.01	4.06	3.93
$k = 0.45$	65.7	70.7	74.5	76.4	3.71	3.76	3.64
$k = 0.50$	67.9	72.7	76.2	78.0	3.46	3.50	3.40
Observed							
Hokkaido Island, 1998–2000[a]	59.3	65.4	69.0	69.9	4.32		
Hokkaido Island, 1950–1957[b]	62.2	69.7	73.8	No data	3.74		

[a]National Salmon Resources Center (2000a, 2000b, 2002).
[b]Hokkaido Salmon Hatchery (1956, 1959).

nese chum salmon increased from ~1% to over 3% during the last quarter of the 20th century (Kaeriyama 1998). By contrast, the return rate of Russian chum salmon decreased from 0.57%–1.90% to 0.12%–0.84% during this same period (Kaev 2000). Therefore, the trends in age and size at maturity are inconsistent with the trend in the return rate. Moreover, the results of our simulation experiments were not influenced by change in mortality much. Although we recognize the importance of the effects of oceanic mortality on age and size at maturity, it seems reasonable to attribute the recent trends in age and size at maturity of chum salmon, in the main, to the change in growth rate.

By contrast, Ricker (1981, 1995) proposed the genetic change hypothesis resulting from size-selective fishing. Size-selective fishing could explain decreasing size at maturity; however, it is difficult for this factor to explain increasing age at maturity. Moreover, the trends in age and size at maturity are inconsistent with the trend to size-selective fishery in Japan (Ishida et al. 1993). From 1952 to 1977, the Japanese salmon fishery operated chiefly in the high seas using gill nets; during this period, age and size at maturity did not change, although gill nets are among the most size-selective fishing gear (Ricker 1981, 1995). After 1978, the Japanese salmon fishery operated chiefly along the coast using set nets, during which time, age at maturity increased and size at maturity decreased, although set nets are probably not size selective (Morita 2003). We believe that an environmental explanation for recent trends in age and size at maturity is more reasonable than an explanation involving genetic selection, at least for Japanese chum salmon.

A genetic change hypothesis should not be ruled out. Genetic selection in relation to fishing has already been shown to account for some of the observed trends in age and size at maturity (Rijnsdorp 1993; Rowell 1993; Haugen and Vøllestad 2001) and it has been verified experimentally (Edley and Law 1988; Reznick 1993; Conover and Munch 2002). Selection for early maturation is more likely to occur, but selection for delayed maturation is also possible when a fishery operates only in the spawning ground (Law and Grey 1989; Heino 1998). Recent studies demonstrated that age-specific threshold size at maturity of Atlantic cod and North Sea plaice have changed over the years (Grift et al. 2003; Barot et al. 2004; Olsen et al. 2004). Moreover, genetic selection in captive salmon has been observed for a variety of traits, including morphology (Fleming et al. 1994), foraging behavior (Yamamoto and Reinhardt 2003), spawning timing (Quinn et al. 2002), and egg size (Heath et al. 2003). Most Japanese chum salmon are produced in artificial enhancement programs (Kaeriyama 1998).

In conclusion, for chum salmon, the age and size at maturity are flexible and depend on growth conditions. Recent trends to increasing age at maturity and decreasing size at maturity can be largely attributed to an adaptive phenotypic response to a reduction in growth rate, which is probably caused by environmental changes. In pursuing the causes of the trends in age and size at maturity, it is necessary to identify the rule of age and size at maturity and then to quantify how age and size at maturity change in response to changing growth rate, before invoking a genetic change hypothesis (cf. Rijnsdorp 1993).

Acknowledgments

We thank E. Sato, T. Takami, and J. Tsuboi for providing helpful information on Japanese chum salmon and T. Saito, Y. Harada, and M. Kaeriyama for helpful discussions. We also thank N. Metcalfe and anonymous referees for improving the paper. This work was supported by Grant-in-Aid No. 16780143 from the Ministry of Education, Culture, Sports, Science, and Technology of Japan.

References

Barot, S., Heino, M., O'Brien, L., and Dieckmann, U. 2004. Long-term trend in the maturation reaction norm of two cod stocks. Ecol. Appl. **14**: 1257–1271.

Barot, S., Heino, M., Morgan, M.J., and Dieckmann, U. 2005. Maturation of Newfoundland American plaice (*Hippoglossoides platessoides*): long-term trends in maturation reaction norms despite low fishing mortality? ICES J. Mar. Sci. **62**: 56–64.

Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V., and Kurashov, V. 1999. The regime concept and natural trends in the production of Pacific salmon. Can. J. Fish. Aquat. Sci. **56**: 516–526.

Berrigan, D., and Koella, J.C. 1994. The evolution of reaction norms: simple models for age and size at maturity. J. Evol. Biol. **7**: 549–566.

© 2005 NRC Canada

Bigler, B.S., Welch, D.W., and Helle, J.H. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). Can. J. Fish. Aquat. Sci. **53**: 455–465.

Campana, S.W. 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. **47**: 2219–2227.

Charnov, E.L. 1990. On evolution of age of maturity and the adult lifespan. J. Evol. Biol. **3**: 139–144.

Conover, D.O., and Munch, S.B. 2002. Sustaining fisheries yields over evolutionary time scales. Science (Washington, D.C.), **297**: 94–96.

Cox, S.P., and Hinch, S.G. 1997. Changes in size at maturity of Fraser River sockeye salmon (*Oncorhynchus nerka*) (1952–1993) and associations with temperature. Can. J. Fish. Aquat. Sci. **54**: 1159–1165.

Edley, M.T., and Law, R. 1988. Evolution of life histories and yields in experimental populations of *Daphnia magna*. Biol. J. Linn. Soc. **34**: 309–326.

Elliott, J.M. 1993. A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an English Lake District stream. Can. Spec. Publ. Fish. Aquat. Sci. No. 118. pp. 109–122.

Fleming, I.A., Jonsson, B., and Gross, M.R. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Can. J. Fish. Aquat. Sci. **51**: 2808–2824.

Fukuwaka, M., and Kaeriyama, M. 1994. A back-calculation method for estimating individual growth of juvenile chum salmon by scale analysis. Sci. Rep. Hokkaido Salmon Hatchery, **48**: 1–9. [In Japanese with an English summary.]

Fukuwaka, M., and Suzuki, T. 2000. Density-dependence of chum salmon in coastal waters of the Japan Sea. North Pac. Anadr. Fish Comm. Bull. **2**: 75–81.

Fukushima, M., Quinn, T.J., and Smoker, W.W. 1998. Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. Can. J. Fish. Aquat. Sci. **55**: 618–625.

Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M., and Dieckmann, U. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Mar. Ecol. Prog. Ser. **257**: 247–257.

Grover, M.C. 2005. Changes in size and age at maturity in a population of kokanee *Oncorhynchus nerka* during a period of declining growth conditions. J. Fish Biol. **66**: 122–134.

Haugen, T.O. 2000. Growth and survival effects on maturation pattern in populations of grayling with recent common ancestors. Oikos, **90**: 107–118.

Haugen, T.O., and Vøllestad, L.A. 2001. A century of life-history evolution in grayling. Genetica, **112–113**: 475–491.

Healey, M.C. 1986. Optimal size and age at maturity in Pacific salmon and effects of size-selective fisheries. Can. Spec. Publ. Fish. Aquat. Sci. No. 89. pp. 39–52.

Heath, D.D., Heath, J.W., Bryden, C.A., Johnson, R.M., and Fox, C.W. 2003. Rapid evolution of egg size in captive salmon. Science (Washington, D.C.), **299**: 1738–1740.

Heino, M. 1998. Management of evolving fish stocks. Can. J. Fish. Aquat. Sci. **55**: 1971–1982.

Heino, M., Dieckmann, U., and Godø, O.R. 2002*a*. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES J. Mar. Sci. **59**: 562–575.

Heino, M., Dieckmann, U., and Godø, O.R. 2002*b*. Measuring probabilistic reaction norms for age and size at maturation. Evolution, **56**: 669–678.

Helle, J.H., and Hoffman, M.S. 1995. Size decline and older age at maturity of two chum salmon (*Oncorhynchus keta*) stocks in western North America, 1972–92. Can. Spec. Publ. Fish Aquat. Sci. No. 121. pp. 245–260.

Hinch, S.G., Healey, M.C., Diewert, R.E., Thomson, K.A., Hourston, R., Henderson, M.A., and Juanes, F. 1995. Potential effects of climate change on marine growth and survival of Fraser River sockeye salmon. Can. J. Fish. Aquat. Sci. **52**: 2651–2659.

Hokkaido Salmon Hatchery. 1956. Age composition, length composition, weight composition and the pattern of the central portion of scales of adult chum salmon migrating into major streams of Hokkaido. Data Rec. No. 105. Hokkaido Salmon Hatchery, Hokkaido, Japan. [In Japanese.]

Hokkaido Salmon Hatchery. 1959. Age composition, length composition, weight composition of adult chum salmon migrating into major streams of Hokkaido (1956–1957). Data Rec. No. 107. Hokkaido Salmon Hatchery, Hokkaido, Japan. [In Japanese.]

Hutchings, J.A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology, **74**: 673–684.

Ishida, Y., Ito, S., Kaeriyama, M., McKinnell, S., and Nagasawa, K. 1993. Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific Ocean and possible causes. Can. J. Fish. Aquat. Sci. **50**: 290–295.

Ishida, Y., Welch, D.W., and Ogura, M. 1995. Potential influence of North Pacific sea-surface temperatures on increased production of chum salmon (*Oncorhynchus keta*) from Japan. Can. Spec. Publ. Fish Aquat. Sci. No. 121. pp. 271–275.

Kaeriyama, M. 1998. Dynamics of chum salmon, *Oncorhynchus keta*, populations released from Hokkaido. North Pac. Anadr. Fish Comm. Bull. **1**: 90–102.

Kaev, A.M. 2000. Recent reduction in chum salmon (*Oncorhynchus keta*) growth and its consequences for reproduction. North Pac. Anadr. Fish Comm. Bull. **2**: 247–253.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES J. Mar. Sci. **57**: 659–668.

Law, R., and Grey, D.R. 1989. Evolution of yields from populations with age-specific cropping. Evol. Ecol. **3**: 343–359.

Mangel, M. 1996. Life history invariants, age at maturity and the feros trout. Evol. Ecol. **10**: 249–263.

Metcalf, J.C., Rose, K.E., and Rees, M. 2003. Evolutionary demography of monocarpic perennials. Trends Ecol. Evol. **18**: 471–480.

Morita, K., and Morita, S.H. 2002. Rule of age and size at maturity: individual variation in the maturation history of resident white-spotted charr. J. Fish Biol. **61**: 1230–1238.

Morita, S.H. 2003. Growth, abundance and maturity of Pacific salmon in the central North Pacific. Ph.D. thesis, Hokkaido University, Hakodate, Japan.

Morita, S.H., Morita, K., and Sakano, H. 2001. Growth of chum salmon (*Oncorhynchus keta*) correlated with sea surface salinity in the North Pacific. ICES J. Mar. Sci. **58**: 1335–1339.

Mylius, S.D., and Diekmann, O. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. Oikos, **74**: 218–224.

National Salmon Resources Center. 2000*a*, 2000*b*, 2002. Database on biological assessment of Pacific salmon populations in Japan. Salmon Databases 8, 9, and 10. National Salmon Resources Center Sapporo, Japan. [In Japanese.]

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., and Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature (London), **428**: 932–935.

Parker, R.R. 1962. Estimations of ocean mortality rates for Pacific salmon (*Oncorhynchus*). J. Fish. Res. Board Can. **19**: 561–589.

Pyper, B.J., and Peterman, R.M. 1999. Relationships among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967–1977. Can. J. Fish. Aquat. Sci. **56**: 1716–1720.

© 2005 NRC Canada

Quinn, T.P., Peterson, J.A., Gallucci, V.F., Hershberger, W.K., and Brannon, E.L. 2002. Artificial selection and environmental change: countervailing factors affecting the timing of spawning by coho and chinook salmon. Trans. Am. Fish. Soc. **131**: 591–598.

Reznick, D.N. 1993. Norm of reaction in fishes. *In* The exploitation of evolving resources. *Edited by* T.K. Stokes, J.M. McGlade, and R. Law. Springer-Verlag, Berlin. pp. 72–89.

Ricker, W.E. 1964. Ocean growth and mortality of pink and chum salmon. J. Fish. Res. Board Can. **21**: 905–931.

Ricker, W.E. 1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. **38**: 1636–1656.

Ricker, W.E. 1995. Trends in the average size of Pacific salmon in Canadian catches. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 593–602.

Rijnsdorp, A.D. 1993. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. Oecologia, **96**: 391–401.

Roff, D.A. 1984. The evolution of life history parameters in teleosts. Can. J. Fish. Aquat. Sci. **41**: 989–1000.

Rowell, C.A. 1993. The effects of fishing on the timing of maturity in North Sea cod (*Gadus morhua* L.). *In* The exploitation of evolving resources. *Edited by* T.K. Stokes, J.M. McGlade, and R. Law. Springer-Verlag, Berlin. pp. 44–61.

Salo, E.O. 1991. Life history of chum salmon. *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 231–309.

Stearns, S.C. 1983. The evolution of life-history traits in mosquitofish since their introduction to Hawaii in 1905: rates of evolution, heritabilities, and developmental plasticity. Am. Zool. **23**: 65–75.

Tanaka, S. 1960. Studies on the dynamics and the managements of fish populations. Bull. Tokai Reg. Fish. Res. Lab. **28**: 1–200. [In Japanese with an English summary.]

Trippel, E.A. 1995. Age at maturity as a stress indicator in fisheries. Bioscience, **45**: 759–771.

Watanabe, K. 1999. Estimation of survival rate of juvenile chum salmon and evaluation of salmon ranching practice in Hokkaido, Japan. Bull. Natl. Salmon Resour. Cent. **2**: 29–37. [In Japanese with an English summary.]

Yamamoto, T., and Reinhardt, U.G. 2003. Dominance and predator avoidance in domesticated and wild masu salmon *Oncorhynchus masou*. Fish. Sci. **69**: 88–94.

Appendix A. Estimation of growth transition matrix *G*.

To obtain the growth transition matrix, we used a stochastic von Bertalanffy growth model (Quinn and Deriso 1999). The expected growth increment during the next year for the individual in size class i, denoted by Δ_i, is

$$\text{(A1)} \quad \Delta_i = (l_\infty - l_i)(1 - e^{-k})$$

where l_i is the approximated size of size class i such that l_i = 30.5, 31.5, 32.5,...,84.5 cm. If the realized growth increment follows a normal distribution, the probability that an individual of size class i will grow to size class j in the next year is

$$\text{(A2)} \quad G_{i,j} = \frac{1}{\sigma\sqrt{2\pi}} \int_{l_j-0.5}^{l_j+0.5} \exp\left[-\frac{(x - l_i - \Delta_i)^2}{2\sigma^2}\right] dx$$

where σ is the standard deviation of the growth increment, σ = 3.120 (observed value). Since the size-class interval was set at 1 cm, individuals in size class j include $l_j \pm 0.5$ cm. We assumed that no fish shrink or grow beyond the maximum size, 85 cm.

Reference

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, Oxford.

© 2005 NRC Canada

Lake level and trophic state variables among a population of shallow Florida lakes and within individual lakes

Mark V. Hoyer, Christine A. Horsburgh, Daniel E. Canfield, Jr., and Roger W. Bachmann

Abstract: Monthly total phosphorus, total nitrogen, and chlorophyll concentrations, Secchi depth, and lake water level data for 84 Florida lakes were used to examine relations between trophic state variables and water level fluctuation. Lake size averaged 566 ha (range 4.0 to 5609 ha), with the period of record for individual lakes averaging 57 months (range 7 to 175 months). Lake level fluctuation for individual lakes averaged 1.3 m (range 0.1 to 3.5 m). The lakes also ranged from oligotrophic to hypereutrophic, with average chlorophyll values for individual lakes ranging from 1 to 97 $\mu g \cdot L^{-1}$. No overall relation between trophic state variables and lake level fluctuation could be found among the population of lakes. However, individual lakes showed direct, inverse, or no significant relations between lake trophic state variables and water level fluctuation, regardless of the magnitude of water level fluctuation. These data suggest that predicting how water level fluctuations will impact trophic state variables among a population of lakes will be difficult, if not impossible, and that any accurate predictions will have to be made after first examining several mechanisms within individual lake systems.

Résumé : Les concentrations mensuelles de phosphore total, d'azote total et de chlorophylle, les profondeurs de Secchi et les données de niveau des eaux dans 84 lacs de Floride nous ont servi à examiner les relations entre les variables du niveau trophique et les fluctuations du niveau d'eau. Les lacs ont en moyenne 566 ha de surface (4,0 ha à 5609 ha); ils ont été suivis individuellement en moyenne pendant 57 mois (7 mois à 175 mois). Les fluctuations des niveaux des lacs individuels sont en moyenne de 1,3 m (0,1 m à 3,5 m). Les lacs varient aussi d'oligotrophes à hypereutrophes et les valeurs moyennes des concentrations de chlorophylle dans les lacs individuels vont de 1 $\mu g \cdot L^{-1}$ à 97 $\mu g \cdot L^{-1}$. Nous ne trouvons pas de relation globale entre les variables de l'état trophique et les fluctuations des niveaux des lacs dans cet ensemble de lacs. Cependant, dans les lacs individuels, il y a des relations positives, négatives et (ou) non significatives entre les variables de l'état trophique et les fluctuations du niveau de l'eau, indépendamment de l'importance de la fluctuation du niveau de l'eau. Ces données laissent croire qu'il est difficile, voire impossible, de prédire comment les fluctuations du niveau de l'eau vont affecter les variables de l'état trophique dans un ensemble de lacs et que toute prédiction précise ne pourra se faire avant d'avoir d'abord examiné plusieurs mécanismes dans des systèmes de lacs individuels.

[Traduit par la Rédaction]

Introduction

Studies examining the ecology of shallow lakes have increased greatly over the last couple of decades, leading to the concept that nutrient-rich shallow lakes can occur in two alternative stable states (Scheffer 1998; Jeppesen et al. 1998). One state is characterized by low transparency and high phytoplankton densities (turbid), and the other by high transparency and abundant submerged vegetation (clear-water state). Many mechanisms working together and independently tend to keep a shallow lake in one state or the other (Scheffer 1998). However, water level fluctuation is thought to be a major factor impacting some of these mechanisms and causing lakes to shift from one state to the other (Scheffer and Jeppesen 1997; Blindlow et al. 1997). For example, the water level of Lake Tamnaren in Sweden was intentionally lowered 1.5 m between 1870 and 1954 to decrease flooding of farmlands (Scheffer 1998). After the water level was decreased, aquatic macrophytes expanded strongly and the lake became famous for its waterfowl. However, in the spring of 1977, the water level rose 0.3 m, leading to dramatic changes in the ecology of the lake. The submersed, floating leafed, and part of the emergent vegetation vanished, after which swans and other aquatic birds dis-

Received 8 November 2004. Accepted 4 August 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 2 November 2005.
J18402

M.V. Hoyer,[1] C.A. Horsburgh, D.E. Canfield, Jr., and R.W. Bachmann. University of Florida, Department of Fisheries and Aquatic Sciences, 7922 NW 71st Street, Gainesville, FL 32653, USA.

[1]Corresponding author (e-mail: mvhoyer@ufl.edu).

 doi: 10.1139/F05-177 © 2005 NRC Canada

appeared from the lake. Because water level changes can completely change the biota of lake systems, scientists participating in an international workshop on shallow lakes systems suggested that water level fluctuation could have an overriding effect on the ecology, functioning, and management of shallow lakes (Coops et al. 2003).

One area of limnological research suggests that changes in water level are very important to sediment resuspension and that water level is a major environmental factor influencing water quality. There are many examples of shallow lakes that have high nutrient concentrations and low water clarity resulting from the resuspension of sediments (Kristensen et al. 1992; Havens et al. 1999; Bachmann et al. 1999). In these and other lakes, individual lakes show increases in nutrient concentrations and decreases in water clarity as lake levels decrease (Noges et al. 1998). For example, decreasing water level caused increases in nutrient and chlorophyll concentrations of Lake Newnan, Florida, by increasing sediment resuspension and internal nutrient loading (Nagid et al. 2001). However, decreasing water levels have also caused decreases in chlorophyll concentration and increases in water clarity because of increasing aquatic macrophyte abundance (Blindlow 1992). There are many examples of increases in aquatic macrophyte abundances as a result of decreasing water level in shallow lakes that cause decreases in nutrient and chlorophyll concentrations and increases in water clarity (Blindlow et al. 1993; Faafeng and Mjelde 1997; Scheffer 1998). Alternately, there are examples of increasing water levels causing decreases in aquatic plant abundance resulting in turbid conditions. Lake Okeechobee is a good Florida example of increasing water level allowing turbid pelagic water to move into the nearshore areas on the edge of the western marshes, increasing turbidity and causing declines in macrophytes (Havens et al. 2004). Thus, two major mechanisms (sediment resuspension and aquatic macrophyte abundance) that can impact nutrient and chlorophyll concentrations and water clarity in shallow lakes work in opposite directions with decreasing or increasing water level.

There are many other mechanisms, e.g., nutrient loading (Dillon 1975), color (Brown et al. 2000), retention time (Garcia de Emiliani 1997), biotic interactions (Gasith and Hoyer 1997), and others (Nagid et al. 2001; Havens et al. 2004), that are also related to water level changes in a lake that may impact trophic state characteristics. These mechanisms alone or in combination may overshadow the impacts of sediment resuspension and macrophyte abundances on nutrient concentrations and water clarity. Thus, water level changes in individual lakes should have differing impacts on nutrient and chlorophyll concentrations and water clarity depending on the lake's unique characteristics. However, if changes in water level drive one overriding mechanism in a population of lakes, thereby influencing nutrient and chlorophyll concentrations and water clarity, then most of the lakes should change in the same direction with increases or decreases in water level. This would provide an additional tool for limnologists attempting to understand and manage shallow lakes.

Limnologists have long sought patterns in lake functioning to provide a basis for predictions to manage lakes, but their approaches to prediction and explanation have often differed (Peters 1991). We decided to examine the impact of changes in lake water levels on total phosphorus (TP), total nitrogen (TN), and chlorophyll (Chl) concentrations and Secchi depth among a population of Florida lakes and within individual Florida lakes. This is important because Florida has over 7700 lakes and water level fluctuation is being proposed by management agencies as a key to maintaining water quality. Emphasizing the importance of water level fluctuation seems reasonable because most Florida lakes are shallow, with the majority of them having mean depths less than 5 m (average mean depth for 360 Florida lakes is 2.99 m; Florida LAKEWATCH 2003).

Table 1. Descriptive statistics for physical, chemical, and aquatic plant variables measured in 84 Florida lakes.

Parameter	Mean	Standard deviation	Minimum	Maximum
No. of months	57	29	7	175
[TP] ($\mu g \cdot L^{-1}$)	21	19	3	105
[TN] ($\mu g \cdot L^{-1}$)	735	533	60	3396
[Chl] ($\mu g \cdot L^{-1}$)	13	18	1	97
Secchi depth (m)	2.2	1.5	0.3	7.1
Mean depth (m)	3.1	1.4	1.2	7.8
Surface area (ha)	566	1089	4	5609
Dynamic ratio	1.03	1.03	0.16	5.92
Range in level (m)	1.3	0.6	0.1	3.5
PAC	27	24	0	94

Note: TP, Total phosphorus; TN, total nitrogen; Chl, chlorophyll; PAC, percent area covered with aquatic plants.

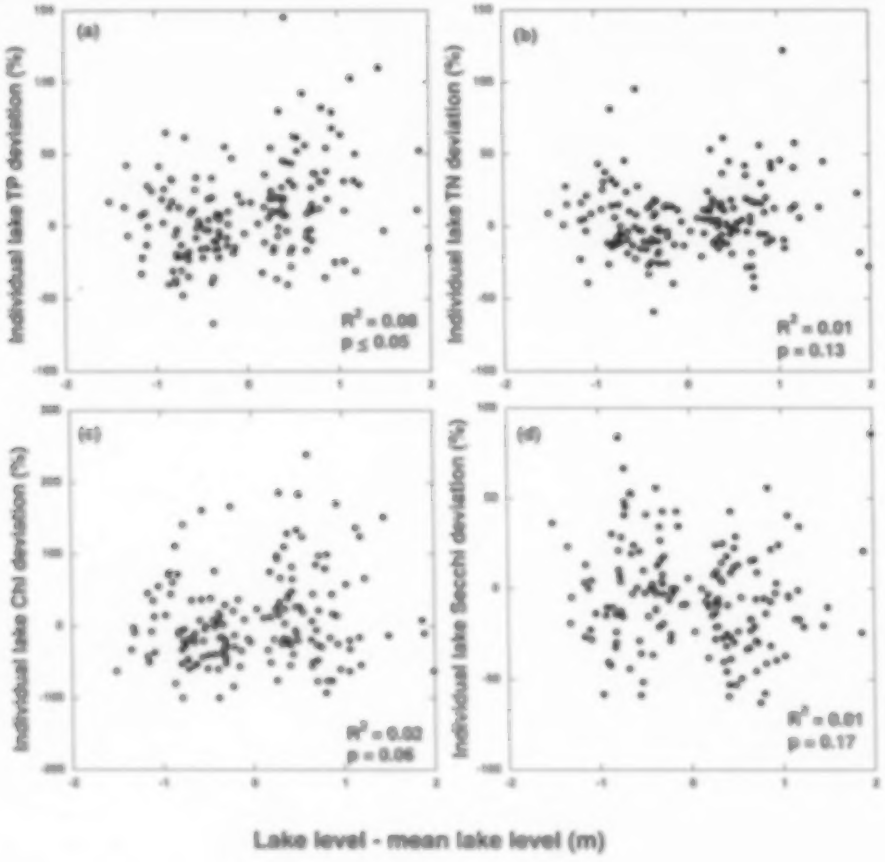
Methods

Florida LAKEWATCH is a citizen volunteer monitoring program started in 1986 with the goal of collecting credible data on TP, TN, and Chl concentrations and Secchi depth from a large number of lakes on a monthly basis (Canfield et al. 2002). The citizens are trained by professionals to collect, prepare, and preserve surface water samples, which are then sent to a laboratory and analyzed. In 1991, a comparative study of 125 lakes found that the data collected by volunteers were comparable to those collected by professionals. Mean Secchi depth and TP, TN, and chlorophyll values obtained by the citizens were strongly correlated ($r > 0.99$) to mean values obtained by the professionals. A detailed description of all methods used in the Florida LAKEWATCH program can be found in Canfield et al. (2002).

Total phosphorus concentrations ($\mu g \cdot L^{-1}$) were determined by the procedures of Murphy and Riley (1962) with a persulfate digestion (Menzel and Corwin 1965). Total nitrogen concentrations ($\mu g \cdot L^{-1}$) were determined by oxidizing water samples with persulfate and determining nitrate nitrogen with second derivative spectroscopy (Crumpton et al. 1992; Bachmann and Canfield 1996). Chlorophyll concentrations ($\mu g \cdot L^{-1}$) were determined spectrophotometrically following pigment extraction with 90% ethanol (Sartory and Grobbelaar 1984) and using the tricromatic equation for chlorophyll *a* (Method 10200 H; APHA 1992). Because we did not

© 2005 NRC Canada

Fig. 1. Plots of monthly deviations (%) from long-term means for total phosphorus (TP), total nitrogen (TN), chlorophyll (Chl) and Secchi depth (Secchi) for individual lakes versus the corresponding monthly deviations (as actual metres) from long-term levels. Only data for the lowest and highest monthly water levels during the period of record for each individual lake were used, yielding two data points for each lake.



correct for pheophytins, we consider measurements to be total chlorophyll.

All five Florida Water Management Districts maintain staff gauges on a number of lakes, and monthly water level data are available corresponding to lakes in the Florida LAKEWATCH program. All monthly lake level measurements corresponding to LAKEWATCH water sampling events were obtained and matched with the individual lake's nutrient, chlorophyll, and water clarity data. A total of 84 lakes had matching monthly water quality and lake level data, with a period of record ranging from 7 to 175 monthly measurements (Table 1). The range in water level fluctuation, which is the difference between the highest and lowest lake level throughout the period of record, ranged from 0.1 to 3.5 m. Water levels in these 84 lakes fluctuated according to the balance between rainfall, runoff, and evaporation. Unless large rainfall events occurred, the monthly changes in water level for individual lakes were small compared with the whole period of record. Available water level data were monthly averages; thus it was not possible to match water level reading and water samples to the same day.

Florida LAKEWATCH professionals measured percent area covered with aquatic plants (PAC) of all 84 lakes on one day during the period of record (Florida LAKEWATCH 2003). PAC was determined according to the methods of Maceina and Shireman (1980). Mean depths for the 84 lakes were estimated from the fathometer transects used to estimate PAC. Surface areas for all 84 lakes were obtained from Shafer et al. (1986) or from bathymetric maps constructed by Florida LAKEWATCH (2003; 56 of the 84 lakes). Maps were created using Trimble Global Positioning System (Trimble Unit Pro XRS with a TSC1 data logger) and a Lowrance depth finder (LMS-350A). Map contours were generated using a kriging technique in Surfer software package (Golden Software, Golden, Colorado).

As a measure of potential sediment resuspension caused by wind-driven waves (Bachmann et al. 2000), we calculated the dynamic ratio (square root of lake surface area (km^2) × mean depth (m)) for each of the 84 lakes. The ratio was also calculated for lower lake levels at each contour (contours were recorded in feet (ft)) of the 56 lakes for which bathymetric maps were available to assess how the dynamic

© 2005 NRC Canada

Table 2. Mean least squares regression statistics (range in parentheses) for lakes that showed significant direct (group 1), inverse (group –1), or no (group 0) relations between actual water level and trophic state variables (TP, total phosphorus; TN, total nitrogen; Chl, total chlorophyll; Secchi, Secchi depth) within individual lakes.

		Regression statistics		
Regression group	No. of lakes	Mean intercept	Mean slope	Mean R^2
TP vs. water level				
TP group –1	9	241 (38 to 463)	–10.7 (–20.5 to –2.3)	0.31 (0.07 to 0.72)
TP group 0	44	32 (–370 to 456)	–0.3 (–8.4 to 10.9)	0.03 (0.0 to 0.10)
TP group 1	31	–223 (–936 to –13)	13.6 (1.8 to 57.1)	0.19 (0.04 to 0.68)
TN vs. water level				
TN group –1	12	9007 (1 001 to 33 414)	–316 (–831 to –280	0.20 (0.07 to 0.53)
TN group 0	41	949 (–6 925 to 26 236)	–7.9 (–696 to 307)	0.04 (0.0 to 0.45)
TN group 1	31	–4099 (–28 426 to –57)	263 (31 to 1583)	0.22 (0.06 to 0.84)
Chl vs. water level				
Chl group –1	8	287 (19 to 1424)	–17.6 (–74.9 to –2.6)	0.20 (0.08 to 0.39)
Chl group 0	52	32 (–370 to 1803)	–0.6 (–45.2 to 13.2)	0.03 (0.0 to 0.17)
Chl group 1	24	–303 (–3174 to –8)	15.1 (1.02 to 168.8)	0.16 (0.04 to 0.56)
Secchi vs. water level				
Secchi group –1	24	27.5 (1.5 to 229)	–1.1 (7.1 to 0.1)	0.24 (0.05 to 0.97)
Secchi group 0	48	1.3 (–147 to 29)	–0.1 (–1.5 to 2.8)	0.03 (0.0 to 0.19)
Secchi group 1	12	–9.1 (–35.5 to –1.1)	0.6 (0.1 to 2.3)	0.30 (0.12 to 0.53)

ratio would change with decreasing water level. Dynamic ratio changes with increasing water level could not be examined because contours above the water level were not available.

The potential area of a lake where submersed aquatic vegetation will grow, assuming light is the limiting factor, can be calculated using a relation between the maximum depth of plant colonization and Secchi depth (Canfield et al.1985) and overlaying this depth on a bathymetric map. The potential PAC was also calculated for each contour to see how it would change with decreasing water level. This was done for the 56 lakes, but potential PAC changes with increasing water level could not be examined because contours above the water level at the time the maps were generated were not available.

To determine if there is one overriding mechanism impacting the relation between nutrient and chlorophyll concentrations and Secchi depth and water level fluctuations among lakes, we calculated the deviation from the long-term mean for each TP, TN, chlorophyll, and Secchi depth monthly measurement within each individual lake. Each deviation was listed as a percent of the lake's long-term mean. The difference between the actual monthly water level and the long-term average water level was also calculated. Plotting all of these data together to look for trends among lakes would not be proper because each lake has a different period of record and the lakes with the longest record would weight the analysis. Thus, for each lake we selected the matched monthly data with the lowest and highest lake level yielding two data points for each lake and then plotted these deviations for trophic state variables against the corresponding deviations in lake level.

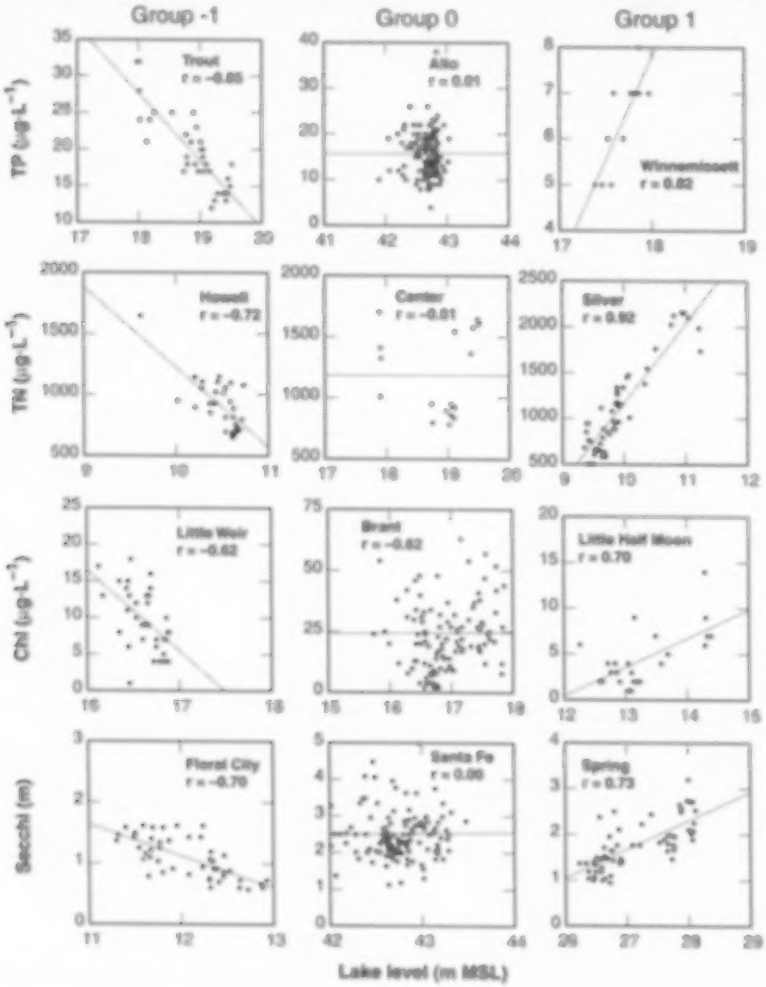
Least squares linear regression was used to determine if each trophic state variable was related to water level fluctuations within each lake, which we considered the experimental unit. These analyses were used to separate lakes into three groups per trophic state variable. Group 1 included lakes that showed significant direct relations, group –1, significant inverse relations, and group 0, no significant relations between individual trophic state variables and corresponding lake level. A two-way analysis of variance with an interaction term (Snedecor and Cochran 1967) was used to determine if trophic state variables (factor 1 values are TP, TN, and chlorophyll concentrations and Secchi depth), group classification (factor 2 values are group –1, group 0, and group 1), and (or) the interaction of these two class variables accounted for significant variance in the range of water level fluctuation for individual lakes, dynamic ratio, and measured PAC. Three separate analyses were done, one for each variable (lake level range, dynamic ratio, and PAC). For each particular factor combination in any one of the analyses, there were 84 replicate observations, each one corresponding to a lake. Dynamic ratio values were transformed to their logarithms (base 10) and PAC values were transformed using an arcsine transformation before statistical analyses to accommodate heterogeneity of variances (Snedecor and Cochran 1967). We used the JMP statistical package (SAS Institute Inc. 2000) for statistical computations and statements of significance are at $p \leq 0.05$.

Results and discussion

The period of record for the 84 individual lakes having both water level and trophic state data ranged from 7 to 175 months, with an average of 57 months (Table 1). The lakes ranged from oligotrophic to hypereutrophic (Forsberg and Ryding 1980), with long-term average chlorophyll concentrations within individual lakes ranging from 1 to 97 $\mu g \cdot L^{-1}$. Overall, chlorophyll concentration averaged 13 $\mu g \cdot L^{-1}$. TP and TN concentrations averaged 21 $\mu g \cdot L^{-1}$ and 735 $\mu g \cdot L^{-1}$, respectively, and individual lake averages ranged from 3 to 105 $\mu g \cdot L^{-1}$ and from 60 to 3400 $\mu g \cdot L^{-1}$, re-

© 2005 NRC Canada

Fig. 2. Plots of total phosphorus (TP), total nitrogen (TN), and chlorophyll (Chl) concentrations and Secchi depth (Secchi) versus corresponding monthly water levels for selected lakes (MSL, mean sea level). Group –1 includes lakes with significant inverse relationships, group 0, no relationships, and group 1, direct relationships between trophic state variables and lake levels.



spectively. Average Secchi depth for individual lakes averaged 2.2 m, with average water clarity readings ranging from 0.3 to 7.0 m.

Overall, the 84 Florida lakes used in this study are shallow, with 90% of the lakes having mean depths < 5 m. The lakes had an average mean depth of 3.1 m, with individual lake mean depths ranging from 1.2 to 7.8 m. The study lakes were also typically small, with 90% of the lakes having surface areas < 2000 ha. The recorded surface areas ranged from 4 to 5600 ha, with an overall average of 566 ha. The average fluctuation in water level during the individual lake's period of record was 1.3 m, with a range of 0.1 to 3.5 m.

If there were one dominant mechanism impacting changes in nutrient and chlorophyll concentrations and Secchi depth with water level changes, then plots of long-term deviations should show significant relations with a positive or negative slope (Fig. 1). Only the deviations for TP concentrations among all lakes were significantly related to water level deviations. However, water level deviation accounting for only 8% of the variance in TP deviations (Fig. 1*a*), and deviations in TN and chlorophyll concentrations and Secchi depth were not significantly related to water level deviations, suggesting that (*i*) more than one mechanism is working within individual lakes among this population of lakes, (*ii*) there are no relations between nutrient and chlorophyll concentrations, Secchi depth, and water level fluctuations among these lakes, or (*iii*) a combination of both.

To examine relations between nutrient and chlorophyll concentrations, Secchi depth, and lake water level within individual lakes, we plotted monthly nutrient and chlorophyll concentrations and Secchi depth measurements against actual monthly water levels (independent variable). For each dependent variable, lakes were found with significant inverse relations, significant direct relations, and no significant relations (Table 2), which may explain why no strong relations

© 2005 NRC Canada

Table 3. Descriptive statistics for groups of lakes that showed significant direct (group 1), inverse (group –1), or no (group 0) relations between actual water level and trophic state variables (TP, total phosphorus; TN, total nitrogen; Chl, total chlorophyll; Secchi, Secchi depth) using least squares regression statistics within individual lakes in each group.

		Range in lake level (m)			Dynamic ratio			PAC		
Regression group	*N*	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
TP vs. water level										
TP group –1	9	1.29	0.70	1.88	0.70	0.29	1.56	19	0	74
TP group 0	44	1.27	0.10	3.50	0.98	0.19	3.56	28	0	93
TP group 1	31	1.27	0.34	3.04	1.19	0.16	5.92	29	0	94
TN vs. water level										
TN group –1	12	1.13	0.38	1.89	1.11	0.19	5.92	27	0	93
TN group 0	41	1.26	0.10	3.50	0.99	0.24	4.24	26	0	74
TN group 1	31	1.34	0.34	2.45	1.05	0.16	3.73	30	0	94
Chl vs. water level										
Chl group –1	8	1.02	0.57	1.53	1.39	0.30	3.56	26	4	52
Chl group 0	52	1.35	0.10	3.50	0.97	0.19	5.92	27	0	94
Chl group 1	24	1.19	0.34	2.40	1.03	0.16	4.24	28	0	92
Secchi vs. water level										
Secchi group –1	24	1.21	0.40	2.13	0.90	0.16	3.63	24	0	92
Secchi group 0	48	1.28	0.10	3.50	1.20	0.19	5.92	29	0	94
Secchi group 1	12	1.35	0.58	2.02	0.60	0.29	0.84	29	0	74

Note: The mean, minimum, and maximum are listed for range in lakes level (m), dynamic ratio, and percent area covered by aquatic plants (PAC). *N* is the number of lakes in each group. A two-way analysis of variance showed that neither trophic state variable nor group classification nor the interaction of these two class variables accounted for significant variance in the range of water level fluctuation for individual lakes, dynamic ratio, or measured PAC.

Table 4. The 25% quantile, median, 75% quantile, and range of calculated dynamic ratios using three different contours from 56 bathymetric maps.

	Quantiles for dynamic ratio			
	25%	Median	75%	Range
Contour 0.0 m	0.3	0.51	1.01	0.07 to 5.39
Contour 0.91 m	0.29	0.55	0.96	0.07 to 5.63
Contour 1.52 m	0.33	0.6	1.12	0.07 to 7.52
Contours 0.91 and 0.0 m	–0.02	0.02	0.1	–0.37 to 1.20
Contours 1.52 and 0.0 m	–0.01	0.06	0.21	–0.58 to 3.64

Note: The quantiles and ranges for the difference in dynamic ratios between contours 0.91 m and 1.52 m and 0.0 m are also listed.

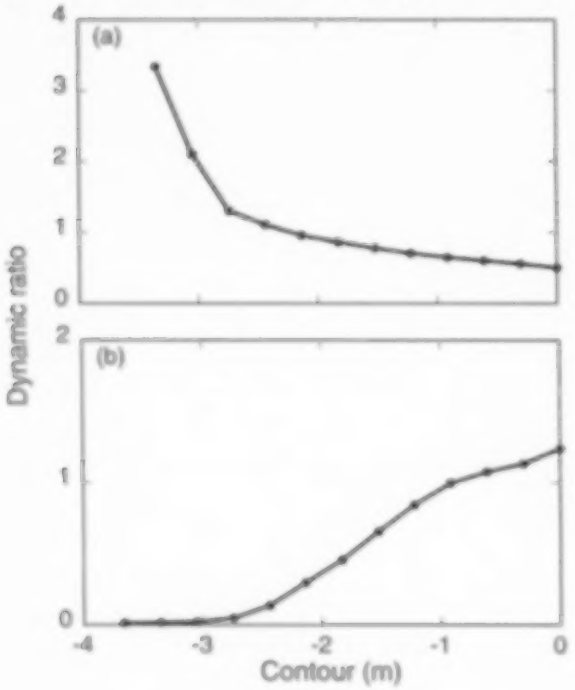
were seen when all of the data were standardized and plotted together (Fig. 1). Some of the significant relations were quite strong (Fig. 2), suggesting that in these lakes, water level could be used as a predictor of nutrient and chlorophyll concentrations and Secchi depth. However, approximately half or more of the lakes showed no significant relation between water level and nutrient and (or) chlorophyll concentrations and (or) Secchi depth (Table 2), clearly indicating that statements regarding the positive or negative influence of water level fluctuation on the water quality of shallow lakes must be made cautiously.

There were only seven lakes that followed conventional trophic state theory in which if nutrient concentrations went up or down significantly with lake water level, then chlorophyll concentrations responded accordingly, and Secchi depth responded inversely to chlorophyll. Examining all other combinations of the relations between trophic state variables and lake water level within individual lakes revealed 31 different groups among all lakes. The largest group was 18 lakes that all showed no relations between each nutrient, chlorophyll, Secchi depth, and lake water level. This examination suggests that several mechanisms may be impacting trophic state variables differently as lake levels change within individual lakes.

Lakes with small (0.2–0.5 m) or large (>0.5 m) changes in water level have been shown to exhibit significant changes in trophic state variables due to several mechanisms (Scheffer 1998; Nagid et al. 2001; Havens et al. 2004). To examine if the magnitude of water level change determines a lakes potential for significant relations between water levels and trophic state variables, lakes were grouped as to whether nutrient and chlorophyll concentrations and Secchi depth showed significant inverse relationships (group –1), no significant relationships (group 0), or significant direct relationships (group 1) with water level (Table 3). A two-way analysis of variance using trophic state variables, group, and the interaction between these two class variables as independent variables and the range in lake level over the period of record as a dependent variable showed no significant effects (Table 3). Thus, although small and (or) large changes

© 2005 NRC Canada

Fig. 3. Dynamic ratio calculated for lower lake water levels at individual depth contours from bathymetric maps of (*a*) Lake Tsala Apopka, Citrus County, Florida, and (*b*) Lake Como, Putnam County, Florida, versus the contour depths.



in water level can impact trophic state variables in lakes (Scheffer 1998; Nagid et al. 2001), predicting how trophic state variables change based on the magnitude that lake levels fluctuate among a large population of shallow Florida lakes can not be demonstrated.

Using a sample of Florida lakes, Bachmann et al. (2000) showed that for lakes with a dynamic ratio > 0.8, the entire lake bed was subjected to wave disturbance at least some of the time. Similar ratios have been used as screening tools to determine which lakes might be susceptible to sediment disturbance by wind-driven waves (Hakanson 1982; Osgood 1988). To examine if dynamic ratio is a factor determining a lake's potential for significant relations between water level and trophic state variables, we used the lake groupings (Table 2) where nutrient and chlorophyll concentrations and Secchi depth showed significant inverse relationships (group –1), no significant relationships (group 0), or significant direct relationships (group 1) with water level. A two-way analysis of variance using trophic state variables, group, and the interaction between these two class variables as independent variables and dynamic ratio as the dependent variable showed no significant effects (Table 3). These data suggest that the dynamic ratio is not an overriding mechanism determining relations between nutrients, chlorophyll, and Secchi depth and water level fluctuations. However, the above analysis assumes that the dynamic ratio does not change with water level fluctuation.

Bathymetric maps were available for a subset of 56 of the 84 lakes used in this study. To test whether the dynamic ratio changes as water level decreases, the maps were used to calculate the dynamic ratio at the 0.0, 0.91 (3 ft), and 1.52 m (5 ft) contours. These contours were selected because they cover approximately 80% of the actual measured ranges in lake level fluctuations. The median dynamic ratio of the 56 lakes showed an increasing trend from 0.51 in the 0.0 m contour to 0.60 in the 1.52 m contour (Table 4). Examining the difference between the 0.0 m contour and both other contours, however, showed that the dynamic ratio would both increase and decrease in individual Florida lakes as water level decreased. For example, Lake Lochloosa shows a dramatic increase in the dynamic ratio as water level decreases, whereas Lake Como shows a decrease in the dynamic ratio as water level decreases (Fig. 3). For approximately 25% of the lakes, the dynamic ratio decreased from 0.0 m to either 0.91 m or 1.52 m contours. We were not able to examine potential changes in the dynamic ratio that might occur with increasing water level because contours were not available above the 0.0 m contour on the day of mapping (Florida's lakes are known for significant increases in water level during floods because of the state's low relief). However, data for this population of lakes clearly indicate that water level fluctuations can increase or decrease the potential for lakes to experience sediment resuspension, depending on the lake's individual morphology. Again, this probably helps explain why no relations were seen when all of the data were standardized and plotted (Fig. 1).

Historically, many studies have shown inverse relations between abundance of submersed aquatic vegetation and trophic state variables (Goulder 1969; Canfield et al. 1984; Jeppesen et al. 1990). To examine if aquatic plant abundance as estimated with PAC is a major factor determining a lake's potential for significant relations between water level and trophic state variables, we used lake groupings where nutrient and chlorophyll concentrations and Secchi depth showed significant relationships (group 1 or group –1) or no significant relationships (group 0) with water level (Table 2). A two-way analysis of variance using trophic state variables, group, and the interaction between these two class variables as independent variables and PAC as a dependent variable showed no significant effects (Table 3). These data for our study lakes, therefore, indicate that the PAC is not the overriding mechanism determining relationships between nutrient and chlorophyll concentrations and Secchi depth and water level fluctuations. The above analysis, however, once again assumes that PAC does not change with water level fluctuation.

To ascertain if the potential PAC value changes as water level decreases, each lake's average Secchi depth was used with an equation from Canfield et al. (1985) to predict the maximum depth of colonization for submersed aquatic plants. We then used this maximum depth of colonization with the bathymetric maps to calculate potential PAC values at the 0.0, 0.91, and 1.52 m contours (~80% of the actual measured ranges in lakes level). The potential PAC of the 56 Florida lakes showed an increase from a median of 49% in the 0.0 m contour to 56% in the 0.91 m contour and 64% in the 1.52 m contour (Table 5). Examining the range of differ-

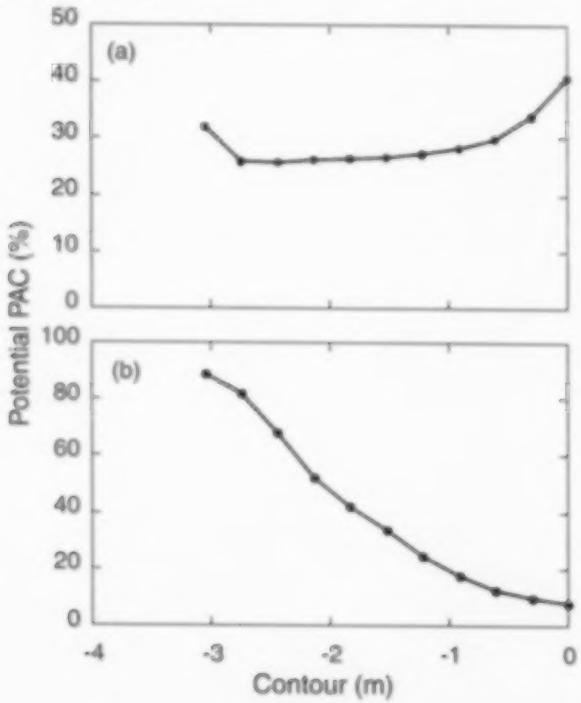
© 2005 NRC Canada

Table 5. The 25% quantile, median, 75% quantile, and range of measured percent area covered with aquatic plants (PAC) and potential PAC using three different contours from 56 bathymetric maps.

	Quantiles for PAC			
	25%	Median	75%	Range
Measured PAC	9	17	32	2 to 93
Potential PAC contour 0.0 m	33	49	66	8 to 100
Potential PAC contour 0.91 m	33	56	84	26 to 100
Potential PAC contour 1.52 m	40	64	93	18 to 100
Potential PAC contours 0.91 m and 0.0 m	1	5	11	−12 to 43
Potential PAC contours 1.52 m and 0.0 m	3	10	22	−14 to 74

Note: The potential PAC was estimated by calculating maximum depth of plant colonization (Canfield et al. 1984) using average Secchi depth values for each lake and overlaying it on the bathymetric maps. The quantiles and ranges for the difference in potential PAC between contours 0.91 m and 1.52 m and potential PAC at 0.0 m are also listed.

Fig. 4. Potential percentage area covered with aquatic plants (potential PAC) calculated at individual contours from bathymetric maps of (*a*) Lake Charlotte, Highlands County, Florida, and (*b*) Lake Harris, Lake County, Florida, versus the individual contour. The potential PAC was estimated by calculating maximum depth of plant colonization (Canfield et al. 1985) using average Secchi depth values for each lake and overlaying it on the bathymetric maps.



ences between the potential PAC at the 0.0 m contour and both other contours, however, showed that potential PAC could both increase and decrease in individual lakes as water level decreases. For example, Lake Charlotte shows a decrease in potential PAC as water becomes deeper, but Lake Harris shows an increase (Fig. 4). Therefore, potential PAC in individual lakes can increase or decrease as lake levels change, depending on lake morphology. It is also important to point out that the median for the actual measured PAC is much less than the median potential PAC for contours 0.0, 0.91, and 1.52 m (Table 5), suggesting that factors other than light can impact a entire lake's PAC, as other authors have suggested (Spence 1982; Duarte and Kalff 1986; Bachmann et al. 2002). Thus, water level fluctuations can either increase or decrease plant abundance, and the ultimate effect on lake trophic state variables can be uncertain despite the well-documented inverse relationship between phytoplankton and aquatic macrophytes.

In conclusion, limnologists have long sought general patterns in lake functioning to aid lake management (Dillon and Rigler 1974; Jones and Bachmann 1976; Peters 1991). Water level fluctuations are often assumed to be a general lake functioning pattern that has an overriding effect on the ecology and management of shallow lakes (Coops et al. 2003). We, however, could find no overall relation between trophic state variables and lake level fluctuation among a population of 84 Florida lakes. Based on our available data, individual lakes can show direct, inverse, and (or) no significant relation between lake trophic state variables and water level fluctuations, regardless of the magnitude of water level fluctuation.

Individual lake studies have shown that sediment resuspension and aquatic macrophyte abundance can impact (both independently and in combination) lake trophic state parameters as lake water levels change. However, in Florida lakes, sediment resuspension (estimated with the dynamic ratio) and potential PAC (assuming light is the limiting factor for plant abundance) can increase or decrease as water level increases or decreases, depending on lake morphology. Many other mechanisms related to water level fluctuations also have the potential to override the importance of sediment resuspension and (or) aquatic plant abundance. Thus, although many scientists continue to emphasize the importance of water level fluctuations, we strongly feel the prediction of the effects of water level fluctuations on lake trophic state parameters will remain difficult without examining several mechanisms within an individual system.

There have been and probably will continue to be debates regarding the best approach towards understanding the limnological functioning of lakes (Lehman 1986; Peters 1986). Some of the philosophical arguments are related to defining

© 2005 NRC Canada

the parameters of interest (e.g., trophic state variables) and understanding the uncertainties associated with predictions (Canfield and Bachmann 1981; Canfield 1983). Other arguments are directly related to how the arguments are constructed. For example, what is a shallow lake (Padisak and Reynolds 2003)? Padisak and Reynolds (2003), in their overview of the role of depth in ecosystem functioning of inland waters, observed there are absolute and relative measures, as well as pragmatic concerns. Lake managers have to be concerned about pragmatic issues, and it is clear based on our study that managers should no longer categorically state that water level fluctuation would improve water quality as measured by trophic state parameters. Although there are general patterns of limnological functioning for the population of Florida lakes (Brown et al. 2000), water level fluctuation is not a predictor of trophic state variables, and individual lake properties must be considered before predictions are made.

Acknowledgments

Financial support for this project was provided by the Florida LAKEWATCH program University of Florida / Institute of Food and Agricultural Services. We thank the many volunteers who donated their time and efforts to collecting the many samples used in this study. This paper is Journal Series No. R-10941 of the Florida Agricultural Experiment Station.

References

APHA. 1992. Standard methods for the examination of water and wastewater. 18th ed. American Public Health Association, Washington, D.C.

Bachmann, R.W., and Canfield, D.E., Jr. 1996. Use of an alternative method for monitoring total nitrogen concentrations in Florida lakes. Hydrobiologia, **323**: 1–8.

Bachmann, R.W., Hoyer, M.V., and Canfield, D.E., Jr. 1999. The restoration of Lake Apopka in relation to alternative states. Hydrobiologia, **394**: 219–232.

Bachmann, R.W., Hoyer, M.V., and Canfield, D.E., Jr. 2000. The potential for wave disturbance in shallow Florida lakes. Lake Reservoir Manag. **16**: 281–291.

Bachmann, R.W., Horsburgh, C.A., Hoyer, M.V., Mataraza, L.K., and Canfield, D.E., Jr. 2002. Relations between trophic state indicators and plant biomass in Florida Lakes. Hydrobiologia, **470**: 219–234.

Blindlow, I. 1992. Long- and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshw. Biol. **28**: 15–27.

Blindlow, I., Andersson, G., Hargeby, A., and Johansson, S.. 1993. Long-term patterns of alternate stable states in two shallow eutrophic lakes. Freshw. Biol. **30**: 159–167.

Blindlow, I., Hargeby, A., and Andersson, G. 1997. Alternate stable states in shallow lakes: what causes a shift. *In* The role of macrophytes in structuring the biological community and biogeochemical dynamics in lakes. *Edited by* E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard, and K. Christoffersen. Springer-Verlag, New York. pp. 353–360.

Brown, C.D., Hoyer, M.V., Bachmann, R.W., and Canfield, D.E., Jr. 2000. Nutrient–chlorophyll relationships: an evaluation of empirical nutrient–chlorophyll models using Florida and northern temperate lake data. Can. J. Fish. Aquat. Sci. **57**: 1574–1583.

Canfield, D.E., Jr. 1983. Prediction of chlorophyll *a* concentrations in Florida lakes: the importance of phosphorus and nitrogen. Water Resour. Bull. **19**: 255–262.

Canfield, D.E., Jr., and Bachmann, R.W. 1981. Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. Can. J. Fish. Aquat. Sci. **38**: 414–423.

Canfield, D.E., Jr., Shireman, J.V., Colle, D.E., Haller, W.T., Watkins, C.E., II, and Maceina, M.J. 1984. Prediction of chlorophyll a concentrations in lakes: the importance of aquatic macrophytes. Can. J. Fish. Aquat. Sci. **41**: 497–501.

Canfield, D.E., Jr., Langeland, K.A., Linda, S.B., and Haller, W.T. 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. J. Aquat. Plant Manag. **23**: 25–28.

Canfield, D.E., Jr., Brown, C.D., Bachmann, R.W., and Hoyer, M.V. 2002. Volunteer lake monitoring: testing the reliability of data collected by the Florida LAKEWATCH program. Lake Reservoir Manag. **18**: 1–9.

Coops, H., Beklioglu, M., and Crisman, T.L. 2003. The role of water-level fluctuations in shallow lake ecosystems — workshop conclusions. Hydrobiologia, **506–509**: 23–27.

Crumpton, W.G., Isenhart, T.M., and Mitchell, P.D. 1992. Nitrate and organic N analysis with second-derivative spectroscopy. Limnol. Oceanogr. **37**: 907–913.

Dillon, P.J. 1975. The phosphorus budget of Cameron Lake, Ontario: the importance of flushing rate to the degree of eutrophy of lakes. Limnol. Oceanogr. **20**: 28–39.

Dillon, P.J., and Rigler, F.H. 1974. The phosphorus–chlorophyll *a* relationship in lakes. Limnol. Oceanogr. **19**: 767–773.

Duarte, C.M., and Kalff, J. 1986. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. Limnol. Oceanogr. **31**: 1072–1080.

Faafeng, B.A., and Mjelde, M. 1997. Clear and turbid water in shallow Norwegian lakes related to submerged vegetation. *In* The role of macrophytes in structuring the biological community and biogeochemical dynamics in lakes. *Edited by* E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard, and K. Christoffersen. Springer-Verlag, New York. pp. 361–368.

Florida LAKEWATCH. 2003. Florida LAKEWATCH annual data summaries 2002. Department of Fisheries and Aquatic Sciences, University of Florida / Institute of Food and Agricultural Sciences, Gainesville, Fla.

Forsberg, C., and Ryding, S.O. 1980. Eutrophication parameters and trophic state indices in 30 Swedish waste-receiving lakes. Hydrobiologia, **88**: 189–207.

Garcia de Emiliani, M.O. 1997. Effects of water level fluctuation on phytoplankton in a river-floodplain lake system (Parana River, Argentina). Hydrobiologia, **357**: 1–15.

Gasith, A., and Hoyer, M.V. 1997. The structuring role of macrophytes in lakes: changing influences along lake size and depth gradients. *In* The role of macrophytes in structuring the biological community and biogeochemical dynamics in lakes. *Edited by* E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard, and K. Christoffersen. Springer-Verlag, New York. pp. 381–392.

Goulder, R. 1969. Interactions between the rates of production of a freshwater macrophyte and phytoplankton in a pond. Oikos, **20**: 300–309.

Hakanson, L. 1982. Lake bottom dynamics and morphometry: the dynamic ratio. Water Resour. Res. **18**: 1444–1450.

Havens, K.E., Hunter, H.J., Lowe, E.F., and Coveney, M.F. 1999. Contrasting relationships between nutrients, chlorophyll *a* and Secchi transparency in two shallow subtropical lakes: Lakes Okeechobee and Apopka (Florida, USA). Lake Reservoir Manag. **15**: 298–309.

© 2005 NRC Canada

Havens, K.E., Sharfstein, B., Brady, M.A., East, T.L., Harwell, M.C., Maki, R.P., and Rodusky, A.J. 2004. Recovery of submerged plants from high water stress in a large subtropical lake in Florida, USA. Aquat. Bot. **78**: 67–82.

Jeppesen, E., Jensen, J.P., Kristensen, P., Søndergaard, M., Mortensen, E., Sortkjaer, O., and Olrik, K. 1990. Fish manipulationas a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. Hydrobiologia, **200–201**: 219–228.

Jeppesen, E., Søndergaard, M., Søndergaard, M., and Christoffersen, K. 1998. The structuring role of submerged macrophytes in lakes. Springer-Verlag. New York.

Jones, J.R., and Bachmann, R.W. 1976. Predictions of phosphorus and chlorophyll levels in lakes. J. Water Pollut. Control Fed. **48**: 2176–2182.

Kristensen, P., Søndergaard, M., and Jeppesen, E. 1992. Resuspension in a shallow eutrophic lake. Hydrobiologia, **228**: 101–109.

Lehman, J.T. 1986. The goal of understanding limnology. Limnol. Oceanogr. **31**: 1160–1166.

Maceina, M.J., and Shireman, J.V. 1980. The use of a recording fathometer for the determination of the distribution and biomass of hydrilla. J. Aquat. Plant Manag. **18**: 34–39.

Menzel, D.W., and Corwin, N. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. **10**: 280–282.

Murphy, J., and Riley, J.P. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta, **27**: 31–36.

Nagid, E.J., Canfield, D.E., Jr., and Hoyer, M.V. 2001. Wind-induced increases in trophic state characteristics of a large (27 km^2), shallow (1.5 m mean depth) Florida lake. Hydrobiologia, **455**: 97–110.

Noges, P., Jarvet, A., Tuvikene, L., and Noges, T. 1998. The budgets of nitrogen and phosphorus in shallow eutrophic Lake Vortsjarv (Estonia). Hydrobiologia, **363**: 219–227.

Osgood, R.A. 1988. Lake mixes and internal phosphorus dynamics. Arch. Hydrobiol. **113**: 629–638.

Padisak, J., and Reynolds, C.S. 2003. Shallow lakes: the absolute, the relative, the functional and the pragmatic. Hydrobiologia, **506–509**: 1–11.

Peters, R.H. 1986. The role of prediction in limnology. Limnol. Oceanogr. **31**: 1143–1159.

Peters, R.H. 1991. A critique for ecology. Cambridge University Press, Cambridge.

Sartory, D.P., and Grobbelaar, J.U. 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia, **114**: 177–187.

SAS Institute Inc. 2000. JMP Statistics and Graphics Guide [computer program]. SAS Institute Inc., Cary, N.C.

Shafer, M.D., Dickinson, R.E., Heany, J.P., and Huber, W.C. 1986. Gazetteer of Florida lakes. Florida Water Resource Research Center Publication No. 96, Gainesville, Fla.

Scheffer, M. 1998. Ecology of shallow lakes. Chapman and Hall, London.

Scheffer, M., and Jeppesen, E. 1997. Alternate stable states. *In* The role of macrophytes in structuring the biological community and biogeochemical dynamics in lakes. *Edited by* E. Jeppesen, Ma. Søndergaard, Mo. Søndergaard, and K. Christoffersen. Springer-Verlag, New York. pp. 397–406.

Spence, D.H.N. 1982. The zonation of plants in freshwater lakes. Adv. Ecol. Res. **12**: 37–125.

Snedecor, G.W., and Cochran, W.G. 1967. Statistical methods. 6th ed. The Iowa State University Press, Ames, Iowa.

© 2005 NRC Canada

Predictive models of benthic invertebrate methylmercury in Ontario and Quebec lakes

M.D. Rennie, N.C. Collins, C.F. Purchase, and A. Tremblay

Abstract: Multivariate analyses on benthic invertebrate methylmercury concentrations ([MeHg]) and water chemistry from 12 Quebec water bodies were used to guide the construction of simple, predictive models of benthic invertebrate [MeHg] in 23 lakes in Ontario and Quebec. Separate predictive models for collector–shredder and predatory benthic invertebrates were constructed using multiple regression and were assessed for their predictive utility by cross-validation. Predatory benthic invertebrate [MeHg] was negatively related to pH and positively related to dissolved organic carbon (DOC) concentration (cross-validation $r^2 = 0.31$). Collector–shredder [MeHg] was positively related to [DOC] only (cross-validation $r^2 = 0.13$). Predictive utility of our models is similar to or surpasses that observed in previously published zooplankton MeHg models tested against independently collected data. Significant environmental variables and their contribution to the overall explanatory power of benthic invertebrate MeHg models are similar to those found in zooplankton models, suggesting that in both pelagic and benthic food webs, pH and DOC are important indicators of MeHg bioavailability. Although seasonal patterns in invertebrate [MeHg] were examined, none was detected. These models represent an effective means of identifying water bodies of interest for researchers and for reconstructing past benthic invertebrate [MeHg] patterns using archived water chemistry data.

Résumé : Des analyses multidimensionnelles des concentrations de méthylmercure ([MeHg]) chez les invertébrés benthiques et de la chimie de l'eau de 12 milieux aquatiques du Québec nous ont guidés dans l'élaboration de modèles simples et prédictifs des concentrations de [MeHg] chez les invertébrés benthiques de 23 lacs de l'Ontario et du Québec. Nous avons construit des modèles distincts pour les invertébrés benthiques collecteurs–déchiqueteurs et les prédateurs à l'aide de régressions multiples et nous avons évalué par validation croisée leur utilité pour la prédiction. Il y a une relation négative entre [MeHg] chez les invertébrés benthiques prédateurs et le pH et une relation positive avec le carbone organique dissous (DOC; r^2 de validation croisée = 0,31). [MeHg] des collecteurs–déchiqueteurs est seulement en corrélation positive avec [DOC] (r^2 de validation croisée = 0,13). Les potentiels de prédiction de nos modèles sont semblables ou supérieurs à ceux des modèles de MeHg du zooplancton tirés de la littérature et évalués avec des données récoltées de façon indépendante. Les variables significatives du milieu et leur contribution au pouvoir explicatif global des modèles de MeHg des invertébrés benthiques sont semblables à ceux trouvés dans les modèles de zooplancton, ce qui laisse croire que le pH et DOC sont d'importants indicateurs de la biodisponibilité de MeHg, tant dans les réseaux alimentaires pélagiques que benthiques. Bien que nous les ayons recherchées, nous n'avons pas trouvé de tendances saisonnières du [MeHg] chez les invertébrés. Ces modèles sont des moyens efficaces pour identifier les milieux aquatiques intéressants pour les chercheurs et pour reconstituer les patterns de [MeHg] du passé chez les invertébrés benthiques à partir de données de qualité de l'eau accumulées en archives.

[Traduit par la Rédaction]

Introduction

Significant mercury (Hg) contamination of lakes that do not receive obvious point-source Hg inputs has been reported in North America and Europe (Cope et al. 1990; Bodaly et al. 1993; Parkman and Meili 1993). Concern over high contaminant levels (including Hg) detected in waterfowl and fish in the latter part of the 20th century initiated numerous government-issued advisories on safe levels of fish and wildlife consumption for humans (e.g., Ontario Ministry of the Environment 2003). The primary source of Hg in these otherwise "pristine" lakes is direct through atmospheric deposition (Rudd 1995) or indirect via terrestrial runoff (Mierle and Ingram 1991; Hintelmann et al. 2002).

Received 2 December 2004. Accepted 15 August 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 2 November 2005.
J18437

M.D. Rennie,[1] **N.C. Collins, and C.F. Purchase.**[2] Department of Biology, University of Toronto at Mississauga, 3359 Mississauga Road N., Mississauga, ON L5L 1C6, Canada.
A. Tremblay. Hydro-Québec Production, Unité Environnement, 75 René-Lévesque West, 3rd floor, Montreal, QC H2Z 1A4, Canada.

[1]Corresponding author (e-mail: mrennie@utm.utoronto.ca).
[2]Present address: Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4J1, Canada.

 doi: 10.1139/F05-181 © 2005 NRC Canada

Yet, organisms in lakes that likely receive similar rates of atmospheric inputs (i.e., are geographically close together) may vary remarkably in Hg concentrations across the same or functionally similar species (Wren and Stephenson 1991; Tremblay et al. 1995; Sonesten 2003). Therefore, factors other than atmospheric deposition must influence bioavailability and accumulation of Hg in aquatic organisms.

The primary means of Hg accumulation for organisms occupying higher trophic positions (such as fish, avian, and mammalian predators) is dietary through the assimilation of organic forms of Hg (principally methylmercury (MeHg)) (Lock 1975; Hall et al. 1997; Lawson and Mason 1998). As well, concentrations of contaminants in aquatic organisms typically increase with trophic position (Jackson 1986; Rowan and Rasmussen 1994; McNicol et al. 1997). There is evidence that Hg concentrations ([Hg]) in fish often correlate strongly with environmental correlates such as pH (Qian et al. 2001; Ikingura and Akagi 2003), dissolved organic carbon concentration ([DOC]) (Cope et al. 1990; Suns and Hitchin 1990; Driscoll et al. 1995), and influx from wetlands (Greenfield et al. 2001). However, because fish and waterfowl assimilate most of their Hg burden from their diet, the correlations detected between environmental factors and their Hg loads cannot be direct. Rather, it is more likely that these correlations reflect causal connections between environmental factors and MeHg assimilation in the prey of fish and waterfowl (Westcott and Kalff 1996; Lawson and Mason 1998).

Despite this observation, comparatively little is known about MeHg accumulation in organisms occupying lower trophic positions, particularly benthic invertebrates, which are common prey for a number of waterfowl and fish species for which consumption advisories have been issued. There is evidence that organic [Hg] in organisms occupying lower trophic levels may be correlated with variation in lake water chemistry, as in fish (Westcott and Kalff 1996). MeHg concentrations ([MeHg]) in primary producers and lake seston also seem to depend on ambient environmental conditions (Lawson and Mason 1998; Morrison and Watras 1999). Freshwater invertebrates occupying lower trophic levels are short-lived relative to fish; therefore, [MeHg] in invertebrates may respond more rapidly to variations in water chemistry compared with that in longer-lived organisms.

Benthic invertebrates play an important role in the transport of Hg in lake food webs, as burrowing species may help clear Hg from sediments (Boddington et al. 1979). Benthic invertebrates are a key food source for a variety of fish and can make up a significant energetic subsidy for piscivorous fish when prey fish are unavailable (Vander Zanden and Vadeboncoeur 2002). Thus, the ability to predict [MeHg] in benthic organisms from easily obtained environmental data could be useful in studying ecosystem Hg loads, rates of Hg transport, and food web dynamics. This is particularly true for examinations of historical data, since measures of benthic invertebrate [MeHg] are scarce prior to 1980.

Environmental factors are likely to explain some degree of variation in benthic invertebrate [MeHg] within or across water bodies. Using data from 12 Quebec water bodies, Tremblay and Lucotte (1997) found that benthic invertebrates in reservoirs had higher [MeHg] than those in natural lakes, and [MeHg] was typically higher in predatory versus nonpredatory invertebrates. Hall et al. (1998) have corroborated these findings. However, reservoir age correlates not just with fish and benthic invertebrate MeHg, but also with lake chemistry parameters such as pH (Ikingura and Akagi 2003). Thus, nonindependence between the status of a water body (lakes versus reservoirs) and its associated water chemistry may have confounded past investigations of relationships between lake water chemistry and invertebrate [MeHg] where data sets included both natural lakes and impoundments.

Although they exist for fish, zooplankton, water, and seston, simple models that describe the relationship between [MeHg] in benthic macroinvertebrates and lake water chemistry are lacking. Past attempts to find such relationships have been limited by a lack of relevant data (Wren and Stephenson 1991) and the wide variation in [MeHg] among benthic organisms observed even within a lake (Back and Watras 1995). The aim of our study was to generate models describing invertebrate [MeHg] based on environmental data typically collected by water-monitoring agencies. Our specific goals were to (*i*) determine the appropriate level of taxonomic or functional resolution for generating benthic invertebrate MeHg models, (*ii*) identify environmental variables most strongly correlated with benthic invertebrate [MeHg], (*iii*) construct empirical models using these correlates, and (*iv*) test the predictive efficacy of these models using cross-validation and by comparing the ability of our models to predict independent data in benthic invertebrate [MeHg] against the predictive efficacy of existing zooplankton [MeHg] models to explain independent zooplankton [MeHg] data. In addition, to determine the effect of exposure to fish digestive enzymes on invertebrate [MeHg], we compared predicted invertebrate [MeHg] estimates with [MeHg] of organisms collected from yellow perch (*Perca flavescens*) stomachs.

Methods

Data sources

The data used in this study include (*i*) published invertebrate [MeHg] and previously unpublished environmental data from 12 water bodies collected by Tremblay and Lucotte (1997) in northwestern Quebec (53–54°N, 70–75°W), (*ii*) published invertebrate [MeHg] data from three lakes at the Experimental Lakes Area in northwestern Ontario (49°35′–49°37′N, 93°36′–93°52′W) collected by Hall et al. (1998), with unpublished environmental data obtained through the Government of Canada Department of Fisheries and Oceans, and (*iii*) invertebrate [MeHg] data collected and analyzed from seven lakes in central and northern Ontario (45–48°N, 78–81°W) in combination with surface water pH and [DOC] collected by either the Ontario Ministry of the Environment or the Ontario Ministry of Natural Resources.

Together, these data represent a wide geographical range of typical lakes and reservoirs found on the Canadian Shield (Appendix A). Variables of interest included organism [MeHg], organism [Hg], sediment [MeHg] and [Hg] (all expressed as nanograms of Hg per gram dry weight), year and month of collection, lake temperature (degrees Celsius), pH, Eh (redox potential reported in millivolts), [DOC] (milligrams per

© 2005 NRC Canada

litre), ammonium (micromoles per litre), and phosphate (micromoles per litre). [DOC] has been shown to approximate 90%–100% of total organic C concentration in boreal lakes (Kolka et al. 1999; Brunberg et al. 2002); therefore, when only total organic C concentration was reported, we estimated [DOC] as equivalent to total organic C (Rennie 2003). [DOC] was also estimated using a relationship between lake colour (measured at 425 nm, converted to platinum colour units (PCU) and reported as such) and [DOC] ($F_{[1,6]} = 18.5$, $p = 0.008$, $r^2 = 0.78$) (Rennie 2003). The relationship can be expressed as

$$(1) \qquad [\text{DOC}] = 0.0985 \times \text{colour} + 3.1715$$

and is similar to those published for other lakes from within our study region (Molot and Dillon 1997).

Invertebrate collections

Benthic invertebrate sampling is described in Tremblay and Lucotte (1997) for Quebec lakes and in Hall et al. (1998) for northwestern Ontario Experimental Lakes Area lakes. Clean techniques were used in both studies to avoid Hg contamination. Invertebrates from the central and northern Ontario lakes were obtained during daylight hours in July 2001 from all seven lakes and additionally in May, July, and August in 2002 from Plastic and Shoe lakes (Rennie 2003). When possible, lakes were sampled on alternate days during each collection period, and equipment was cleaned between visits to avoid cross-contamination. Benthic invertebrates were collected using clean kick-and-sweep nets from four to eight sites around each lake to obtain sufficient mass for analyses. Invertebrates and associated debris were stored in acid-washed 591-mL glass jars sealed with acid-washed polyethylene lids and kept on ice until they were returned to the laboratory for sorting and identification.

Benthic invertebrates were separated into coarse taxonomic groups using clean acid-washed Teflon utensils within 2–4 h of collection. Anisopterans, corixids, gerrids, and gyrinids were classified functionally as predators and amphipods, chironomids, ephemeropterans, and trichopterans as collectors–shredders. Composite samples were produced for each sampling date by grouping organisms from common taxonomic groups across all sites of a lake on a given day to achieve sufficient mass for [MeHg] determination. Samples were rinsed with deionized water, blotted with ultralow Hg Kimwipes™, placed in acid-washed 20-mL glass scintillation vials, and frozen at –20 °C for later analysis. Because no effort was made to allow benthic invertebrates to clear their guts before analysis, organism [MeHg] may include [MeHg] from gut contents.

Stomach contents were also collected from yellow perch in 2001 and 2002 from Shoe and Plastic lakes (Rennie 2003). Fish were euthanized, stomachs were removed, and contents were carefully placed into clean acid-washed 1.5-mL scintillation vials. Vials were sealed and stored at –20 °C until analysis. Samples were examined to determine the primary constituents of gut contents before analysis.

Organic Hg analyses

Only organic forms of Hg (principally monomethylmercury) are biomagnified in aquatic food chains (Mason et al. 1995; Lawson and Mason 1998; Lawrence et al. 1999). Although the fraction of MeHg in the total Hg pool of aquatic ecosystems is relatively small (Watras et al. 1995*b*), the MeHg fraction of total Hg in fish occupying higher trophic positions often approaches 90%–100% MeHg (Monteiro et al. 1991; Bloom 1992; Kannan et al. 1998). Thus, studies of Hg transfer focusing on upper trophic organisms can use comparatively simple total Hg measurements as a reliable index of MeHg. However, the organic Hg fraction in both fish and invertebrates occupying lower trophic positions is much more variable and rarely equivalent to total [Hg] values (Lasorsa and Allengil 1995; Tremblay and Lucotte 1997; Mason et al. 2000). Therefore, organic forms of Hg must be measured directly in food web biomagnification studies involving zooplankton and benthos.

[MeHg] in invertebrates has been shown to be equivalent to measures of organic [Hg] (Paterson et al. 1998). Therefore, we chose to analyze samples for organic [Hg] as an estimate of [MeHg] in invertebrates, consistent with the methodology reported elsewhere (Hall et al. 1998). Benthic invertebrate MeHg analyses are as described in Tremblay and Lucotte (1997) for Quebec lakes and in Hall et al. (1998) for Ontario Experimental Lakes Area lakes.

Organic [Hg] for invertebrates collected from our seven Ontario lakes and for those collected from fish stomach contents was determined using methods similar to those reported by Paterson et al. (1998). Briefly, invertebrates were placed in 20-mL preweighed, acid-washed glass scintillation vials and weighed. Wet tissues were dried at 50 °C to constant weight. To homogenize the samples, dried tissues were ground with a glass rod. To avoid contamination between samples, glass rods were rinsed with Hg-free deionized water, soaked in concentrated H_2SO_4 for approximately 30 s, rinsed again in deionized water, and then wiped dry with a Kimwipe™. Homogenized invertebrate tissues were suspended in 5 mL of deionized water to which 2 mL of 3 mol $KBr \cdot L^{-1}$ and 3 mL of 0.65 mol $CuSO_4 \cdot L^{-1}$ were added. The mixture was then shaken for 30 min to release bound organic Hg from invertebrate tissues. A 5-mL aliquot of 3:2 dichloromethane–hexane was added. Samples were shaken for 24 h to extract organically bound Hg from the samples and left overnight to settle. Four millilitres of the organic layer (containing the organic Hg from the sample) was removed and placed in 20-mL acid-washed glass digestion tubes. A 2-mL aliquot of 4:1 HNO_3–H_2SO_4 was then added to the extract, which was then digested at 250 °C for 4–6 h to convert organic Hg to inorganic Hg. Samples were then diluted with 10 mL of Hg-free deionized water and preserved with 200 µL of concentrated BrCl (Bloom and Crecelius 1983) until analysis. Samples were treated with 40 µL of 30% hydroxylamine hydrochloride immediately before analysis. Total [Hg] values were determined using an automated Tekran model 2600 mercury analyzer compliant with US Environmental Protection Agency (2000) method 1631. Reagent and analytical blanks were determined and subtracted from all samples and biological reference standards.

To assess the quality of MeHg data, we also ran a certified biological reference standard from the National Research Council of Canada, DORM-2. The average value (±1 SE) for DORM-2 over all organic Hg analyses, based on 27 runs, each consisting of two to five replicate digests, was 4.06 ± 0.14 µg Hg·g dry weight^{-1}, which is within 10% of the nomi-

© 2005 NRC Canada

Table 1. Distances from discriminant analysis between taxa.

	Collectors–shredders				Predators			
Taxa	Amp	Chi	Eph	Tri	Ani	Cor	Ger	Gyr
Amp	—	0.0170	0.0366	0.0014	*0.0001*	*0.0001*	*0.0001*	*0.0001*
Chi	0.9601	—	0.5022	0.2956	*0.0001*	*0.0001*	*0.0001*	*0.0001*
Eph	0.7285	0.1362	—	0.6507	*0.0001*	*0.0001*	*0.0001*	*0.0001*
Tri	1.2123	0.1945	0.0621	—	*0.0001*	*0.0001*	*0.0001*	*0.0001*
Ani	*5.6216*	*2.776*	*2.4095*	*1.7172*	—	0.0028	0.0497	0.0754
Cor	*7.2801*	*3.2034*	*3.4143*	*2.5812*	0.6838	—	0.6426	0.0001
Ger	*7.3745*	*3.4318*	*3.4681*	*2.6072*	0.4053	0.0597	—	0.0001
Gyr	*4.3121*	*2.5261*	*1.8472*	*1.3474*	0.3214	1.8684	1.4355	—

Note: The bottom triangular matrix consists of distance measures between taxa, and the top triangular matrix contains probabilities of similarities between taxa. Taxa are represented by the first three letters in the group name: Amp, amphipods; Chi, chironomids; Eph, ephemeropterans; Tri, trichopterans; Ani, anisopterans; Cor, corixids; Ger, gerrids; Gyr, gyrinids. Comparisons between functional groups (predators versus collectors–shredders) are italicized.

nal value reported by the National Research Council of Canada (4.47, SD = 0.32).

Statistical analyses

Data for the 12 Quebec water bodies were used to determine the appropriate taxonomic resolution of models and to identify which environmental variables were most important in explaining variation in organism [MeHg]. Pearson and Spearman correlation coefficients for all pairwise comparisons of variables were compared to help identify nonlinear relationships and variables in need of transformation. Organism [Hg] and [MeHg], sediment [Hg] and [MeHg], ammonium, and phosphate were all log-transformed to establish normality in each of the individual variables of interest. Linearity between variable pairs was assessed both visually and through agreement of Spearman with Pearson correlation coefficients.

Objective 1: appropriate resolution for benthic invertebrate [MeHg] models

To achieve this objective, we applied a discriminant analysis to benthic invertebrate [Hg] and [MeHg] (independent variables) to determine the degree to which we could classify organism types (dependent variables) from our observations in multivariate space. We examined the efficacy of this discrimination on two taxonomic levels: first, on the eight taxa of organisms encountered in this data set and, second, based on organism trophic status. Discriminant analyses were carried out using SAS (SAS Institute Inc. 1989). Collectors–shredders made up 42.6% of the total 225 observations, and predators made up 57.3% of all observations.

Objective 2: environmental variables associated with benthic invertebrate [MeHg]

To identify environmental variables most strongly correlated with benthic invertebrate [MeHg], the data were examined in a canonical redundancy analysis (CRA) to examine relationships between our multiple levels of invertebrate [MeHg] (separated by taxonomy based on results from discriminant analysis in objective 1) and the environmental variables that they experienced across invertebrate trophic levels (see Methods, Data sources for a list of environmental variables examined in the analysis). A binary variable was also included to describe water bodies based on their flooding history. Values for organism [MeHg] were sorted by site, and site-specific averages were obtained for groups of benthic invertebrates under study (both by taxa and by functional group). This reduced our total number of observations from 225 to 42. Of the 42 sites, 20 were from lakes and 22 were from reservoirs. Thus, the CRA included as many dependent variables as organisms under study and 11 environmental variables. Observations with missing values for organism [MeHg] were removed from the analysis. CRA were performed using SAS (SAS Institute Inc. 1989); Monte Carlo simulation probabilities and plots from CRA were obtained using redundancy analysis in CANOCO version 4.02 (Centre for Biometry, Wageningen, Netherlands), which is an equivalent procedure to CRA in SAS. Lastly, models were simplified to include only those environmental variables showing a large degree of explanatory power on invertebrate [MeHg] based on the magnitude of correlations with the first axis describing organism [MeHg]. Because our objective was to generate predictive models based on readily available data, we limited the selection of environmental variables to those that are commonly measured and available to researchers.

Objective 3: constructing empirical models

We added data from 11 water bodies in Ontario to our 12 Quebec water bodies and compiled a database consisting of organism [MeHg], lake pH, and lake DOC. As in the previous analysis, organism [MeHg] was log-transformed. Multiple observations within lakes were initially averaged such that each lake would have a single value for pH, DOC, and functional group MeHg (Appendix A). Each observation of either predator or collector–shredder [MeHg] represents the average over one to four taxonomic groups, each of which is the average of one to nine measurements of organism [MeHg] from a given sampling event (Appendix A). Taxonomic groups were weighted equally within a given functional group. Multiple regressions (linear, ordinary least squares) were applied to examine empirical relationships in which log-transformed organism [MeHg] was considered a function of pH, [DOC], and the interaction between the two. Nonsignificant interaction terms and then independent variables were removed in a stepwise fashion until all remaining terms in the model were significant (hereafter referred to as

© 2005 NRC Canada

independent models). Multiple regressions were carried out using SYSTAT (Systat Software Inc. 1998).

Objective 4: testing predictive efficacy

For cross-validation, we expanded the data set to include multiple samples taken from lakes, where multiple samples differed in the month and year in which they were obtained (Appendix A). We repeated the procedure outlined above to find the models of benthic invertebrate [MeHg] in these expanded data sets that included only significant independent variables. This procedure increased the sample size from 23 to 70 and facilitated the cross-validation of our models (hereafter referred to as expanded models). For approximately 30% of the observations in the expanded data sets, measurements of either pH or [DOC] were not made on the date that organisms were sampled. In these cases, we replaced missing values with monthly averages of pH and [DOC] calculated from within the lake in question. pH and [DOC] were not significantly correlated with one another (independent data set, $r = -0.12$, $p = 0.62$; expanded data set, $r = -0.07$, $p = 0.57$).

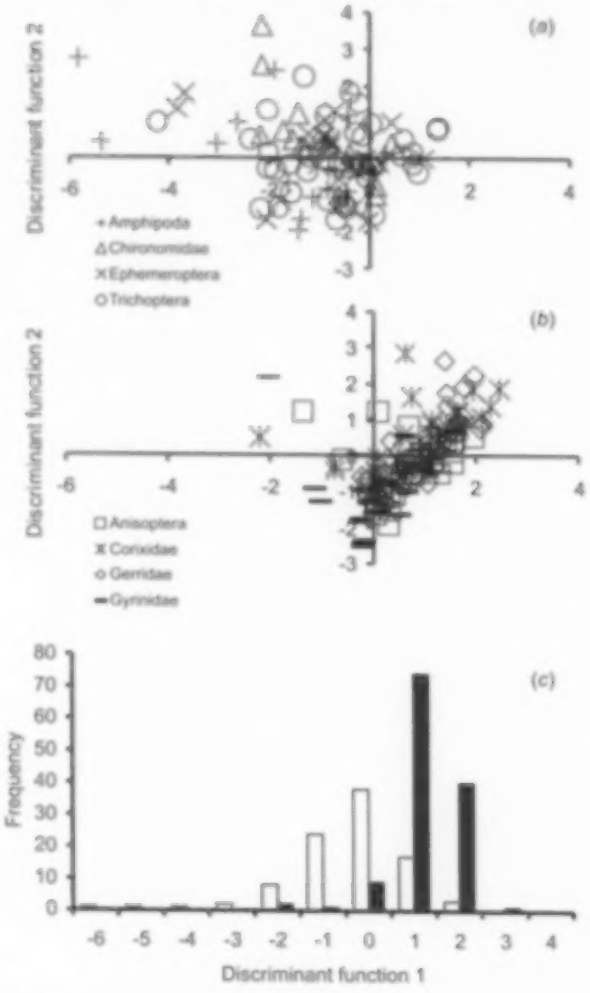
To cross-validate our models, all observations from one selected lake were removed from the data set and data from the remaining lakes were used to generate a statistical model. This model was then tested for its ability to accurately predict the data from the lake that was excluded from the model generation. This procedure was repeated sequentially so that data from each lake were in turn excluded from model generation and predicted independently. After independent predicted values were accumulated for every data point, we estimated the r^2 for cross-validation, Xr^2, as

$$(2) \quad Xr^2 = 1 - (\Sigma[y_{obs} - y_{predicted}]^2 / SS_T)$$

where y_{obs} is the observed value of organism [MeHg] excluded from model generation, $y_{predicted}$ is the value of organism [MeHg] predicted from the subset of data from which the observed values were excluded, and SS_T is the total sum of squares estimated as the variance of organism [MeHg] times $N - 1$, where N is the number of observations used to generate the model.

Lastly, we used 22 independently collected zooplankton [MeHg] and water chemistry data to test the predictive efficacy of two previously published zooplankton models (Westcott and Kalff 1996; Garcia and Carignan 1999) so as to compare the relative performance of our models against others that also relate invertebrate [MeHg] to pH and [DOC]. Previously published zooplankton and (or) environmental data were obtained from Tremblay et al. (1998), Paterson et al. (1998), Back et al. (2003), Gorski et al. (2003), and Watras and Bloom (1992). Daytime samples of zooplankton were taken from four central/northern Ontario lakes using a 0.5-m-diameter plankton net with a 150-μm mesh. Nets were cleaned with Citranox between lakes to avoid cross-contamination. Predatory organisms were removed from samples of two lakes (Plastic and Shoe lakes) but not removed from the other two. Values of Xr^2 were calculated using eq. 2 using the difference between the predicted values of zooplankton [MeHg] calculated from published models compared with actual values observed in independent zooplankton [MeHg] data. Prediction limits (95%) were calculated around predicted organism [MeHg] for all multiple regression models (Sokal and Rohlf 1995).

Fig. 1. Comparisons between invertebrate taxa along the first two discriminant functions: (*a*) collectors–shredders and (*b*) predators separated for clarity. (*c*) Frequency of scores along discriminant function 1 showing separation between invertebrate trophic levels. Open bars, collectors–shredders; solid bars, predators. Invertebrates collected from Quebec reservoirs and lakes, 1992–1995.



Results

Objective 1: appropriate level of resolution for MeHg models

Using our eight taxa as our classification variable, the discriminant function demonstrated a poor but significant separation between taxa (Wilks' $\lambda = 0.4929$, $F_{[14,426]} = 12.91$, $p < 0.0001$). Statistical similarities always occurred among organisms belonging to the same functional groups (Table 1; Figs. 1*a* and 1*b*). Although some differences were observed between organisms in the same functional group, differences between functional groups were always significant (Table 1). SAS cross-validates each observation in the data set by clas-

© 2005 NRC Canada

Fig. 2. Ordination plot from CRA of invertebrate trophic level on environmental factors form Quebec lakes and reservoirs, 1992–1995. Points are individual site scores. Thick lines are invertebrate MeHg concentration; thin lines are environmental variables. Sites in the upper left diagonal of the plot are from reservoirs, and sites in the lower right diagonal are from natural lakes.

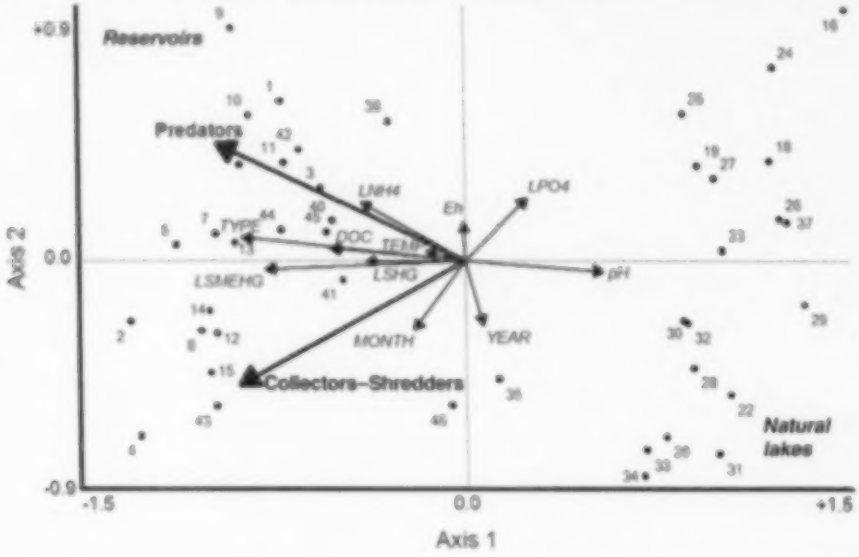


Table 2. Correlations between environmental variables and first two axes describing organism [MeHg] in CRA, with lake type removed.

	Organism [MeHg]	
Environmental variable	Axis 1	Axis 2
Year	–0.0832	0.2863
Month	0.1945	0.2942
Temperature	0.1586	–0.0475
pH	**–0.5526**	**0.0693**
Eh	0.0158	–0.1685
DOC	**0.5429**	**–0.0746**
$\log_{10}$(sediment [Hg])	0.3977	–0.0124
$\log_{10}$(sediment [MeHg])	***0.7939***	***0.01***
$\log_{10}(NH_4)$	0.4272	–0.2703
$\log_{10}(PO_4)$	–0.2366	–0.2626

Note: Bold/italicized values are significant regression coefficients in univariate multiple regression models. Bold variables appear to be most important in all factors examined based on magnitude of correlations with the first axis describing organism [MeHg]. Eh, redox potential.

sifying it using a discriminant function calculated from all observations in the data set but excluding the observation in question. No group of organisms fared well under this cross-validation model; the lowest classification error rate observed was for corixids, which were misclassified only 46% of the time, and all other groups of organisms had classification error rates greater than 56%.

The discriminant analysis was rerun after classifying organisms into only two groups: predators and collectors–shredders. Again, the overall discriminant model was significant (Wilks' $\lambda = 0.6201$, $F_{[2,219]} = 67.09$, $p < 0.0001$) (Fig. 1c). The standardized distance between the two groups was highly significant ($p < 0.0001$). The cross-validation model fared much better under this broader classification, indicating large differences between these groups. Collectors–shredders had approximately three times the error rate in classification than did predators, but at 24% and 8%, respectively, the amount of overlap between functional groups was dramatically less compared with differences among taxa (Fig. 1). Organism [MeHg] explained almost three times more variation in the discriminant function than did organism [Hg] (organism [MeHg], $r^2 = 0.26$; organism [Hg], $r^2 = 0.08$). Mean organism [MeHg] and [Hg] were both significantly different between functional groups ($p < 0.0001$). Based on the clear distinction between benthic invertebrate functional group [MeHg], we chose to develop separate predictive models for predators and collectors–shredders.

Objective 2: selection of environmental variables

The CRA of organism [MeHg] on environmental variables was significant (Wilks' $\lambda = 0.073$, $F = 7.08$, df = 22, $p < 0.0001$). A Monte-Carlo simulation testing the significance of the first canonical axis yielded a p value of 0.005 (based on 199 iterations). Univariate multiple regressions were also significant for both groups of organisms based on environmental variables (collectors–shredders, $r^2 = 0.72$, $p < 0.0001$; predators, $r^2 = 0.84$, $p < 0.0001$). Environmental variables that were important in correlations with [MeHg] of both collectors–shredders and predators were water-body type, pH, [DOC], and sediment [MeHg] (Fig. 2). These variables represent the longest vectors of all environmental variables in the triplot, and all occur along the same plane (Fig. 2). These variables were also strongly correlated with their own principal canonical axis, as well as with the principal canonical axis describing [MeHg] of benthic invertebrates (Table 2). The first environmental canonical variable explained 72.2% of the variation in organism [MeHg], the second added only 5.5% to the explained variation.

© 2005 NRC Canada

Initially, lake type appeared to be the most important variable considered in explaining benthic invertebrate [MeHg], being the only one to yield statistically significant regression coefficients in univariate multiple regressions of environmental variables on organism [MeHg] ($p < 0.0001$). As well, sites were well separated based on lake type alone; organisms from reservoirs occurred on the left-hand side of the triplot, whereas organisms from natural lakes occurred on the right (Fig. 2). We attempted to examine these models after adjusting for the effect of lake type using partial CRA. However, doing so made the statistical model insignificant (Wilks' $\lambda = 0.4122$, $F = 1.162$, df = 20, $p = 0.07$). Additionally, correlations between all environmental variables and organism [MeHg] proved weak. This was due to the fact that lake type is strongly correlated with lake pH, [DOC], and sediment [MeHg] (Fig. 3) (*t* tests between lakes and reservoirs: pH, $p << 0.0001$; [DOC], $p = 0.0007$; $\log_{10}$ sediment [MeHg], $p << 0.0001$; all tests, df = 44, $p_{crit} = (0.025/3) = 0.008$).

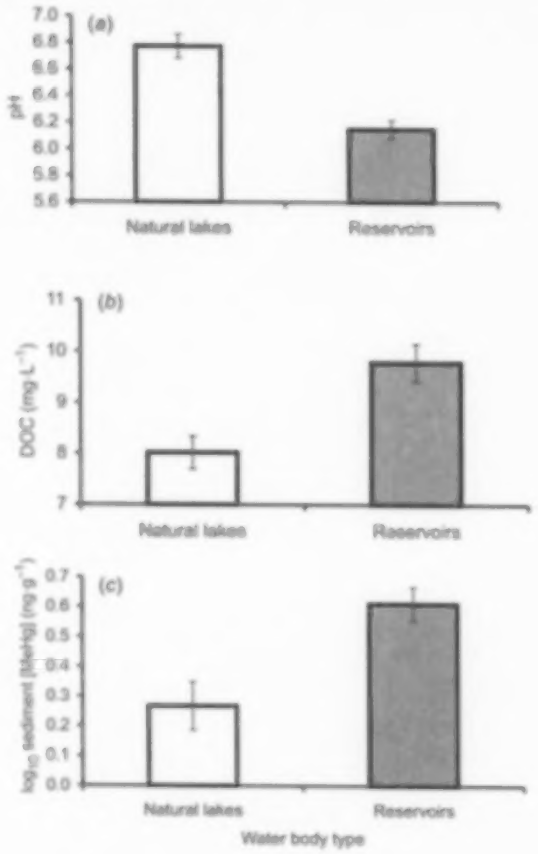
Repeating the CRA with the exclusion of the variable describing lake type yielded a significant model (Wilks' $\lambda = 0.200$, $F = 3.7088$, df = 20, $p < 0.0001$), although reduction in the estimated F statistic reflected a loss of explanatory power due to the loss of the lake type variable. Values of r^2 in the univariate models when lake type was removed fell to 62% and 66%, respectively, for collectors–shredders and predators. From this analysis, we concluded that the inclusion of the lake type variable was masking the effects of other important environmental variables (as per Graham 2003), as the majority of the explanatory power of the lake type variable appeared to be explained by correlation with the other environmental variables listed above. Without lake type, sediment [MeHg], pH, and [DOC] once again appeared as the strongest variables on the first environmental axis (Table 2), each explaining about 20% more variation than in the model including lake type, although sediment [MeHg] was the only significant variable in univariate multiple regressions ($p = 0.0016$) (Fig. 2) (Appendix B).

Sediment [MeHg] occurs infrequently at best in published data or government databases relative to other strongly correlated variables in this analysis. Therefore, to generate models that would be practical given existing available data, we chose to limit our CRA to variables that were strong correlates in the initial analyses and common in lake databases. Models that included only month of collection, pH, and [DOC] were significant (Wilks' $\lambda = 0.467$, $F = 5.67$, df = 6, $p < 0.0001$), and pH and [DOC] were significant terms in models with sediment [MeHg] removed ($p < 0.1$) (as per Graham 2003). r^2 values of univariate models describing invertebrate [MeHg] for collectors–shredders and predators with only these variables were 0.34 and 0.46, respectively. Because these variables alone explained more than half the variation of models with all environmental variables included, and because they are among the most commonly collected of the environmental variables considered here, we chose them to build our predictive models.

Objective 3: empirical models

Both independent models of organism [MeHg] were statistically significant based on only one or two water chemistry variables (Table 3). Coefficients for models based on independent and expanded data sets were similar, and standard errors of coefficient estimates for both procedures overlapped considerably within functional groups. The predator model explained 43% of the overall variation in predatory benthic invertebrate [MeHg] from pH and [DOC] in expanded data sets, representing our most conservative estimate of explained variation (Table 3; Fig. 4*a*). Partial r^2 values were 0.27 for [DOC] and 0.15 for pH, indicating that [DOC] played the major role in predicting predator [MeHg]. The collector–shredder model explained 26% of the overall variation in collector–shredder [MeHg] from [DOC] in expanded data sets (Table 3; Fig. 4*b*). The month of collection did not affect [MeHg] of invertebrate functional groups in expanded data sets (Appendix B); therefore, the month of collection was not considered further.

Fig. 3. Patterns of (*a*) pH, (*b*) [DOC], and (*c*) sediment [MeHg] between natural lakes and reservoirs in Quebec. Error bars are ±1 SE.



Objective 4: model cross-validation and comparison

Our models describe independent data as well as or better than other existing models describing invertebrate [MeHg] based on pH and [DOC]. Cross-validation demonstrated that our models explained 31% of the variation in independent predator data and 13% of the variation in independent

© 2005 NRC Canada

Table 3. Predictive equations of organism [MeHg] from lake chemistry parameters and associated statistical parameters.

Model No.	Model	df	F	p	r^2	r^2_{adj}	Xr^2	SE_{yxt}
1	$\log(MeHg_p) = 3.461(\pm0.546) - 0.261(\pm0.079)pH + 0.043(\pm0.014)DOC$	2, 19	10.78	<0.001	0.531	0.482	—	0.180
2	$\log(MeHg_p) = 3.113(\pm0.364) - 0.214(\pm0.054)pH + 0.053(\pm0.010)DOC$	2, 65	24.11	<<0.0001	0.426	0.408	0.312	0.240
3	$\log(MeHg_{cs}) = 1.184(\pm0.192) + 0.055(\pm0.022)DOC$	1, 19	6.59	0.019	0.257	0.218	—	0.180
4	$\log(MeHg_{cs}) = 1.209(\pm0.116) + 0.062(\pm0.013)DOC$	1, 62	22.22	<<0.0001	0.264	0.252	0.126	0.305
5	$MeHg_z = 449.64 - 47.41pH + 146.35\log(\text{water colour})$	2, 22	39.29	0.0001	0.73	nr	np	65.61
6	$\log(MeHg_z) = 3.52(\pm0.25) + 0.62(\pm0.15)\log(DOC)$	1, 23	nr	0.0005	0.43	nr	0.244	0.23

Note: r^2_{adj}, adjusted r^2 values according to statistical software; Xr^2, cross-validated r^2 values. Models 1 and 3 are based on lake-wide averages, and models 2 and 4 are based on repeated measures within lakes. Cross-validation was carried out on expanded data sets only for benthic invertebrate models (models 2 and 4). Model 5 is from Westcott and Kalff (1996); model 6 is from Garcia and Carignan (1999). Partial r^2 values for the cross-validation predator model (model 2) are 0.27 and 0.15 for DOC and pH, respectively. Subscripts: p, predator; cs, collector–shredder; z, zooplankton; nr, not reported by the authors of the model; np, not possible to calculate given independent data (value less than zero).

collector–shredder data (Table 3). These values are comparable with those obtained for existing zooplankton models predicting independent zooplankton data ($N = 22$) (Table 3; Fig. 5). Xr^2 could not be calculated for the Westcott and Kalff (1996) model owing to large differences between observed and predicted values in independent zooplankton data (Fig. 5*d*). The Garcia and Carignan (1999) model had an $Xr^2 = 0.24$, which falls between the values calculated for our predator and collector–shredder models. However, a large proportion (at least 50% of observations) of zooplankton [MeHg] data for both previously published models fall outside 95% prediction limits (Figs. 5*c* and 5*d*). In contrast, two independent data points of benthic invertebrate [MeHg], pH, and [DOC] obtained from Gorski et al. (2003) fell within the 95% prediction limits of our relationships (Fig. 5).

Although our models appear to underestimate slightly collector–shredder benthic invertebrate [MeHg] from reservoirs, no such bias is evident for predators, and both models appear to accurately describe benthic invertebrates from natural lakes (Figs. 5*a* and 5*b*). Data from reservoirs were consistently underestimated by the Garcia and Carignan (1999) model, with all observations from reservoirs falling above 95% confidence intervals (Fig. 5*c*). In contrast, the Westcott and Kalff (1996) model described reservoirs well, with all observations from reservoirs falling within 95% confidence intervals (Fig. 5*d*).

Observed values of [MeHg] for benthic invertebrates collected from perch stomach contents fall within the general distribution around predictive models as the invertebrate MeHg data (Figs. 5*a* and 5*b*). Some variation was observed between years in collectors–shredders collected from fish stomachs, but considered together, invertebrates collected from stomachs generally fall within the range of predicted values for a given DOC concentration in those lakes. Neither zooplankton model accurately predicts zooplankton [MeHg] collected from fish stomachs (Fig. 5), as at least half of these observations fell outside the 95% confidence intervals of these models.

Discussion

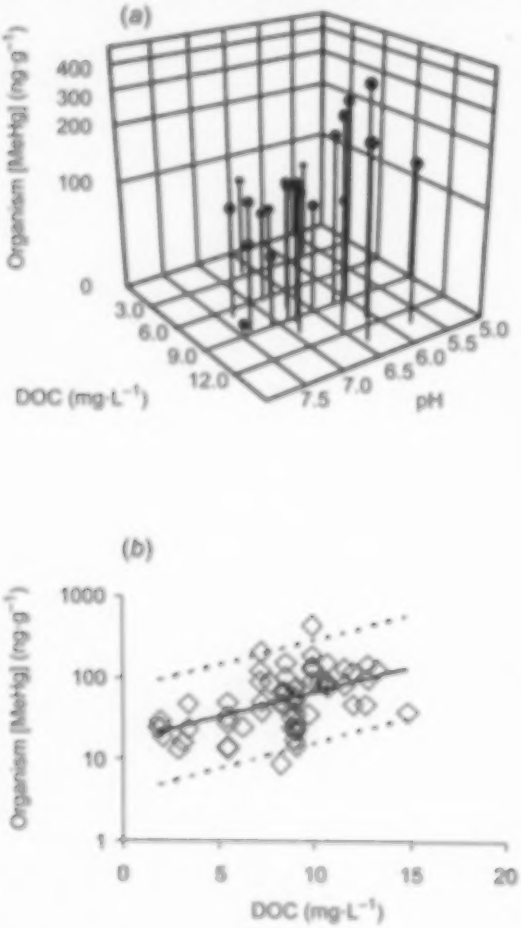
Selection of appropriate model resolution

Benthic invertebrate [MeHg] values were most distinct among functional groups, whereas differentiation based on taxa proved to be generally unreliable. This supports previous approaches that make comparisons between benthic invertebrate [MeHg] at the functional group level (Tremblay and Lucotte 1997; Hall et al. 1998). Previous studies have also shown a significant effect of reservoir age on organism [MeHg] (Tremblay and Lucotte 1997; Hall et al. 1998; Ikingura and Akagi 2003). Our data indicate that lake chemistry alone may explain much of the variation in benthic invertebrate [MeHg] previously attributed to water-body status (lakes versus reservoirs), as excluding lake type caused the explanatory power in our CRA models to fall by only 18% and 10% for the predator and collector–shredder models, respectively. This was likely a result of lake type being significantly correlated with the three environmental variables that also explained the largest amount of variation in benthic invertebrate [MeHg] (Graham 2003). Unfortunately, because of the observed colinearity between impoundment and other environmental variables observed in this and other studies (Ikingura and Akagi 2003), as well as a current lack of alternative data sets with which to evaluate these models, we are unable to distinctly rule out the possibility that some other factor besides pH or [DOC] also associated with lake type may be a contributing factor to our results. We hope that this research stimulates further investigation among systems with wider ranges of pH, [DOC], and benthic invertebrate [MeHg] within each lake type (reservoirs only or natural lakes only) to better evaluate the generality of these models to many aquatic systems.

As expected, [DOC] and pH were important explanatory variables in relationships with benthic invertebrate [MeHg]. Besides previously cited observations in zooplankton (Westcott and Kalff 1996; Garcia and Carignan 1999), [DOC] and pH have also been found to explain a significant

© 2005 NRC Canada

Fig. 4. Relationships describing benthic invertebrate [MeHg] with environmental correlates in (*a*) predators and (*b*) collectors–shredders. The broken lines in Fig. 4*b* represent 95% prediction limits for collector–shredder [MeHg] from a given DOC value.



proportion of the variation in fish [Hg] standardized for size (Cope et al. 1990; Suns and Hitchin 1990; Qian et al. 2001). There is, however, disagreement as to whether water chemistry or lake productivity ultimately plays a more significant role in dictating [Hg] in fish (Kidd et al. 1999; Sonesten 2001; Essington and Houser 2003). [DOC] may also be important in binding free MeHg, which can in turn be taken up by filter-feeding organisms (Watras and Bloom 1992; Hintelmann et al. 1995; Morrison and Watras 1999). Other studies have identified pH and [DOC] as important correlates of [MeHg] values in lake water, where [DOC] and pH together explained 80%–90% of the variation in waterborne [Hg] and [MeHg] (Watras et al. 1995*b*). Concentrations of organic matter correlate positively with sediment [Hg] and methylation rates of sulfate-reducing bacteria (Jackson 1988*b*), and organic matter transported from catchments to lakes is a significant source of Hg in lakes (Mierle and Ingram 1991). Thus, greater inputs of humic matter from watersheds can increase the available pool of inorganic Hg for methylation by bacteria (Jackson 1988*a*). Lower pH also increases the binding capacity of MeHg to lake seston (Hintelmann et al. 1995), and pH is generally negatively correlated with waterborne [MeHg] (Hintelmann et al. 1995; Watras et al. 1995*a*; Morrison and Watras 1999). Similarly, low pH may stimulate methylation rates of bacteria (Xun et al. 1987). [DOC] and pH also appear to be important in the transport of waterborne MeHg into phytoplankton; uptake rates of MeHg by algae are positively affected by the presence of organic ligands possessing sulfhydryl groups, such as thiourea and cysteine (Lawson and Mason 1998), and the binding capacity of sulfhydryl groups for MeHg increases at low pH (Rabenstein and Fairhurst 1975).

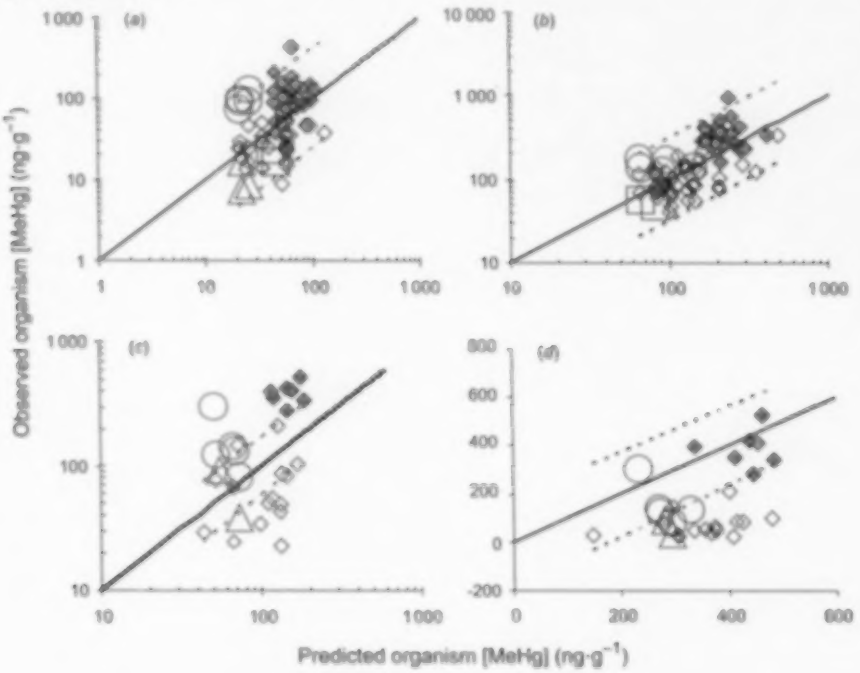
The transfer of MeHg from primary consumers up aquatic food chains is largely dietary (Lawson and Mason 1998) because of the strong affinity of MeHg to sulfhydryl-containing amino acids in the bodies of organisms (Harris et al. 2003) and the slow rate of MeHg elimination from organisms (Trudel and Rasmussen 1997). Organisms exposed to unusually high levels of aqueous MeHg (i.e., Visman et al. 1995) may absorb MeHg directly from waterborne exposure, although concentrations required for this to occur are much greater than those observed in either natural lakes or reservoirs.

This evidence together suggests that water pH and DOC can directly affect both MeHg availability and rates of transfer at the base of aquatic food webs. Furthermore, if assimilation rates from one trophic level to the next are relatively constant across ecosystems, then pH and DOC may directly affect the [MeHg] of aquatic organisms at multiple trophic levels, including benthic invertebrates, by controlling MeHg uptake and availability at the base of aquatic food webs. Collector and shredder organisms typically feed on epiphyton and aquatic macrophtyes. Detritivores such as amphipods (also represented in the collector–shredder model) feed on dead organic matter, which is also capable of taking up waterborne MeHg (Lock 1975). Uptake of MeHg by dead organic matter is passive, as it is likely to be in both algae and seston (Lawson and Mason 1998). Therefore, dead organic matter, algae, and seston are likely to have similar rates of MeHg assimilation and may be affected similarly by water chemistry. If so, models of [MeHg] for zoobenthos based on water chemistry should be similar to those for zooplankton, as both benthic invertebrates and zooplankton assimilate MeHg at similar rates when feeding on diets to which they are adapted (Lawson and Mason 1998). A comparison of partial r^2 values between benthic invertebrate models and those reported by Westcott and Kalff (1996) support this hypothesis. Partial r^2 values for the zooplankton model indicated that water colour explained the majority of [MeHg] variation in zooplankton (Westcott and Kalff 1996). Similarly, DOC (a variable strongly correlated with water colour in these lakes) was three times more important than pH in explaining benthic predator [MeHg] and was the only significant variable in the benthic collector–shredder MeHg model.

The month of collection did not explain a significant proportion of the variation in benthic invertebrate [MeHg], indicating no seasonal trend (Appendix B). This contrasts with other studies that have found significant seasonal effects in zooplankton (Monson and Brezonik 1998; Garcia and Carignan 1999). Studies examining seasonal patterns of sta-

© 2005 NRC Canada

Fig. 5. Observed versus predicted values of organism [MeHg] (diamonds) from cross-validated models of invertebrate (*a*) collectors–shredders and (*b*) predators, as well as for independent zooplankton data predicted from published empirical relationships reported by (*c*) Garcia and Carignan (1999) and (*d*) Westcott and Kalff (1996). Note the differences in scale among axes. Triangles (2001 data) and circles (2002 data) are [MeHg] of organisms collected from fish stomachs. Squares are values from Gorski et al. (2003). The broken lines represent 95% prediction limits of organism [MeHg] for a given *X* or set of *X*. Shaded symbols, reservoirs; open symbols, lakes.



ble isotopes have also observed large variation in zooplankton isotopic ratios over seasonal time scales that were not observed in benthic organisms (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1996). This may be due in part to short generation times (i.e., weeks to months) and fast turnover rates in pelagic zooplankton compared with benthic invertebrates (i.e., months to years). Thus, compared with zooplankton, benthic invertebrate [MeHg] may be less sensitive to variations in water chemistry over seasonal time scales.

Predictive efficacy of benthic invertebrate MeHg models

Our empirical models of benthic invertebrate [MeHg] performed well in predicting independent data compared with existing models of zooplankton [MeHg]. Benthic invertebrate Xr^2 values were similar to those for zooplankton using the Garcia and Carignan (1999) model. Although our collector–shredder model appears to slightly underestimate benthic invertebrate [MeHg] in reservoirs, the model still accurately describes invertebrates from natural lakes, and the predator model appears to accurately describe organisms from both water-body types. Additionally, this bias is nowhere near as large as was observed in the two zooplankton models, where a large proportion of our independent data fell outside the 95% prediction limits. Data from two lakes in the immediate geographic region of lakes reported by Westcott and Kalff (1996) were overestimated (observed versus predicted: Plastic Lake, 77.8 versus 277.5 ng·g^{-1}; Shoe lake, 146.8 versus 297.2 ng·g^{-1}), with Plastic Lake falling outside the 95% prediction limits of their model. Although their model describes MeHg in cladocerans, the discrepancies that we observed could not be caused by the accidental inclusion of predator organisms in our samples, as inclusion of these organisms should produce a deviation in the direction opposite to that observed. Watras and Bloom (1992) reported individual MeHg concentrations for filter-feeding cladocerans, but predicted values for this water body are also overestimated by the Westcott and Kalff (1996) model by an order of magnitude (observed versus predicted: Little Rock Lake, acidified basin, 67.5 versus 373.7 ng·g^{-1}; reference basin, 25.0 versus 307.3 ng·g^{-1}) and also fall outside 95% prediction limits of the model. In comparison, two data points collected from benthic invertebrates in Michigan lakes (Gorski et al. 2003) fell within the 95% prediction limits of both of our benthic invertebrate models.

The poor fit of our independent zooplankton data to the two zooplankton models likely results from the fact that our independent observations span a much wider range both geographically and taxonomically than the data used to generate either of the zooplankton models and that our application of these models arguably goes beyond the scope of their initial purpose. For instance, the Garcia and Carignan (1999) model was originally designed to describe zooplankton from lakes that had sustained recent burns in their catchments. As

© 2005 NRC Canada

well, our data varied slightly in the taxonomic resolution of zooplankton analyzed compared with the models being tested. Westcott and Kalff (1996) analyzed MeHg in cladoceran filter-feeding zooplankton only. With the exception of the two lakes from the region sampled by Westcott and Kalff (1996) and data reported by Watras and Bloom (1992), all of our independent zooplankton data come from bulked zooplankton samples, as reported by Garcia and Carignan (1999). Regardless, no systematic variation was observed due to potential differences in the level of classification of zooplankton with either model.

Although a large proportion of the effect of impoundment on benthic invertebrate [MeHg] appears to be explained by water chemistry, the same cannot be said for zooplankton. In our independent data set, zooplankton [MeHg] from reservoirs was typically higher than predicted by the Garcia and Carignan (1999) model but was described well by the Westcott and Kalff (1996) model. However, zooplankton [MeHg] from natural lakes in our data were typically underestimated by both models (although less so for the Garcia and Carignan (1999) model). Given the large separation of zooplankton [MeHg] that we observed between lakes and reservoirs, impoundment effects on zooplankton (and thus perhaps on other organisms reliant on the pelagic food web) may go beyond simple changes in water chemistry due to upland flooding. An increase in the concentration of suspended particulate matter is often observed in reservoirs and may account for elevated levels of zooplankton [MeHg] that occupy them (Tremblay et al. 1998).

Of the two models that we report in this study, the overall better fit of the predator model may be due to the fact that the collector–shredder functional group designation assumes a much narrower range of feeding habits than actually occurs in nature. Predatory forms of both trichopterans and chironomids are known to inhabit lakes within the range of this study, but our course taxonomic identification assumed that all trichopterans and chironomids encountered were collectors–shredders. Despite these optimistically simple assumptions regarding the feeding habits of organisms in these groups, our models provide high predictive performance relative to the reported average ability of ecologists to explain variation in biological variables of interest (Moller and Jennions 2002).

These models, although statistically significant, offer at best ballpark estimates of benthic invertebrate [MeHg], as evidenced by reported Xr^2 and predictive 95% confidence limits around models. Although these models cannot substitute for actual measures of invertebrate [MeHg], they may allow researchers to identify potential benthic invertebrate MeHg "hotspots" (in lakes that do not receive obvious point-source contamination) based on very basic environmental data and may also allow estimation of benthic invertebrate [MeHg] from historic data sets where these data are absent.

Because [MeHg] in fish tissues is generally higher by an order of magnitude than that of their food, one might expect that Hg contamination of invertebrates would occur in the stomachs of fish. However, for the two lakes for which we have data, [MeHg] measured from stomach contents of fish were similar to estimates for invertebrates collected directly from the lake. This was not the case for zooplankton collected from fish stomachs when predicted with existing zooplankton models, where only half of these observations fell within the 95% confidence intervals of the models. However, this rate is similar to that observed for independent zooplankton data collected directly from the lake. Therefore, we can only say that these existing zooplankton models predict independent zooplankton [MeHg] data collected from fish stomachs, as well as independent zooplankton [MeHg] data collected from lakes.

Acknowledgements

We thank G. Morgan for coordinating the collection of environmental data, staff at the many Ontario Ministry of Natural Resources district offices for making these data available, D. Jackson and B. Shuter for helpful advice on statistical approaches, many people at the Canadian Department of Fisheries and Oceans Experimental Lakes Area for providing environmental data, G. Meirle at the Ontario Ministry of the Environment for his expertise on Hg in the environment, Hydro Quebec for providing environmental data, E. Garcia for discussions regarding their models, M. Curtis, J. LaRose, and N. Kelton for help in the field, and B. Branfireun for discussions, contacts, and a cleanroom. We also thank W.G. Sprules and L.C. Grapentine for insightful editorial comments on a previous draft of this manuscript. This work was supported by a Natural Sciences and Engineering Resaearch Council of Canada strategic grant.

References

Back, R.C., and Watras, C.J. 1995. Mercury in zooplankton of northern Wisconsin lakes — taxonomic and site-specific trends. Water Air Soil Pollut. **80**: 931–938.

Back, R.C., Gorski, P.R., Cleckner, L.B., and Hurley, J.P. 2003. Mercury content and speciation in the plankton and benthos of Lake Superior. Sci. Total Environ. **304**: 349–354.

Bloom, N.S. 1992. On the chemical form of mercury in edible fish and marine invertebrate tissue. Can. J. Fish. Aquat. Sci. **49**: 1010–1017.

Bloom, N.S., and Crecelius, E.A. 1983. Determination of mercury in seawater at sub-nanogram per liter levels. Mar. Chem. **14**: 49–59.

Bodaly, R.A., Rudd, J.W.M., Fudge, R.J.P., and Kelly, C.A. 1993. Mercury concentrations in fish related to size of remote Canadian Shield lakes. Can. J. Fish. Aquat. Sci. **50**: 980–987.

Boddington, M.J., de Freitas, A.S.W., and Miller, D.R. 1979. Effect of benthic invertebrates on the clearance of mercury from sediments. Ecotoxicol. Environ. Saf. **3**: 236–244.

Brunberg, A.K., Nilsson, E., and Blomqvist, P. 2002. Characteristics of oligotrophic hardwater lakes in a postglacial land-rise area in mid-Sweden. Freshw. Biol. **47**: 1451–1462.

Cabana, G., and Rasmussen, J.B. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proc. Natl. Acad. Sci. U.S.A. **93**: 10844–10847.

Cope, W.G., Wiener, J.G., and Rada, R.G. 1990. Mercury accumulation in yellow perch in Wisconsin seepage lakes — relation to lake characteristics. Environ. Toxicol. Chem. **9**: 931–940.

Driscoll, C.T., Blette, V., Yan, C., Schofield, C.L., Munson, R., and Holsapple, J. 1995. The role of dissolved organic carbon in the chemistry and bioavailability of mercury in remote Adirondack lakes. Water Air Soil Pollut. **80**: 499–508.

© 2005 NRC Canada

Essington, T.E., and Houser, J.N. 2003. The effect of whole-lake nutrient enrichment on mercury concentration in age-1 yellow perch. Trans. Am. Fish. Soc. **132**: 57–68.

Garcia, E., and Carignan, R. 1999. Impact of wildfire and clear-cutting in the boreal forest on methyl mercury in zooplankton. Can. J. Fish. Aquat. Sci. **56**: 339–345.

Gorski, P.R., Cleckner, L.B., Hurley, J.P., Sierzen, M.E., and Armstrong, D.E. 2003. Factors affecting enhanced mercury bioaccumulation in inland lakes of Isle Royale National Park, USA. Sci. Total Environ. **304**: 327–348.

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology, **84**: 2809–2815.

Greenfield, B.K., Hrabik, T.R., Harvey, C.J., and Carpenter, S.R. 2001. Predicting mercury levels in yellow perch: use of water chemistry, trophic ecology, and spatial traits. Can. J. Fish. Aquat. Sci. **58**: 1419–1429.

Hall, B.D., Bodaly, R.A., Fudge, R.J.P., Rudd, J.W.M., and Rosenberg, D.M. 1997. Food as the dominant pathway of methylmercury uptake by fish. Water Air Soil Pollut. **100**: 13–24.

Hall, B.D., Rosenberg, D.M., and Wiens, A.P. 1998. Methyl mercury in aquatic insects from an experimental reservoir. Can. J. Fish. Aquat. Sci. **55**: 2036–2047.

Harris, H.H., Pickering, I.J., and George, G.N. 2003. The chemical form of mercury in fish. Science (Wash., D.C.), **301**: 1203.

Hintelmann, H., Welbourn, P.M., and Evans, R.D. 1995. Binding of methylmercury compounds by humic and fulvic acids. Water Air Soil Pollut. **80**: 1031–1034.

Hintelmann, H., Harris, R., Heyes, A., Hurley, J.P., Kelly, C.A., Krabbenhoft, D.P., Lindberg, S., Rudd, J.W.M., Scott, K.J., and St. Louis, V.L. 2002. Reactivity and mobility of new and old mercury deposition in a boreal forest ecosystem during the first year of the METAALICUS study. Environ. Sci. Technol. **36**: 5034–5040.

Ikingura, J.R., and Akagi, H. 2003. Total mercury and methylmercury levels in fish from hydroelectric reservoirs in Tanzania. Sci. Total Environ. **304**: 355–368.

Jackson, T.A. 1986. Methyl mercury levels in a polluted prairie river lake system — seasonal and site-specific variations, and the dominant influence of trophic conditions. Can. J. Fish. Aquat. Sci. **43**: 1873–1887.

Jackson, T.A. 1988*a*. Accumulation of mercury by plankton and benthic invertebrates in riverine lakes of northern Manitoba (Canada) — importance of regionally and seasonally varying environmental factors. Can. J. Fish. Aquat. Sci. **45**: 1744–1757.

Jackson, T.A. 1988*b*. The mercury problem in recently formed reservoirs of northern Manitoba (Canada) — effects of impoundment and other factors on the production of methyl mercury by microorganisms in sediments. Can. J. Fish. Aquat. Sci. **45**: 97–121.

Kannan, K., Smith, R.G., Lee, R.F., Windom, H.L., Heitmuller, P.T., Macauley, J.M., and Summers, J.K. 1998. Distribution of total mercury and methyl mercury in water, sediment, and fish from south Florida estuaries. Arch. Environ. Contam. Toxicol. **34**: 109–118.

Kidd, K.A., Paterson, M.J., Hesslein, R.H., Muir, D.C.G., and Hecky, R.E. 1999. Effects of northern pike (*Esox lucius*) additions on pollutant accumulation and food web structure, as determined by $\delta^{13}C$ and $\delta^{15}N$, in a eutrophic and an oligotrophic lake. Can. J. Fish. Aquat. Sci. **56**: 2193–2202.

Kolka, R.K., Grigal, D.F., Verry, E.S., and Nater, E.A. 1999. Mercury and organic carbon relationships in streams draining forested upland peatland watersheds. J. Environ. Qual. **28**: 766–775.

Lasorsa, B., and Allengil, S. 1995. The methylmercury to total mercury ratio in selected marine, fresh-water, and terrestrial organisms. Water Air Soil Pollut. **80**: 905–913.

Lawrence, A.L., Mcaloon, K.M., Mason, R.P., and Mayer, L.M. 1999. Intestinal solubilization of particle-associated organic and inorganic mercury as a measure of bioavailability to benthic invertebrates. Environ. Sci. Technol. **33**: 1871–1876.

Lawson, N.M., and Mason, R.P. 1998. Accumulation of mercury in estuarine food chains. Biogeochemistry, **40**: 235–247.

Lock, R.A.C. 1975. Uptake of methylmercury by aquatic organisms from water and food. *In* Sublethal effects of toxic chemicals on aquatic animals. *Edited by* J.H.Koeman and J.J.T.W.A. Strik. Elesevier Scientific Publishing Company, Amsterdam, Netherlands. pp. 61–79.

Mason, R.P., Reinfelder, J.R., and Morel, F.M.M. 1995. Bioaccumulation of mercury and methylmercury. Water Air Soil Pollut. **80**: 915–921.

Mason, R.P., Laporte, J.M., and Andres, S. 2000. Factors controlling the bioaccumulation of mercury, methylmercury, arsenic, selenium, and cadmium by freshwater invertebrates and fish. Arch. Environ. Contam. Toxicol. **38**: 283–297.

McNicol, D.K., Mallory, M.L., Mierle, G., Scheuhammer, A.M., and Wong, A.H.K. 1997. Leeches as indicators of dietary mercury exposure in non-piscivorous waterfowl, in central Ontario, Canada. Environ. Pollut. **95**: 177–181.

Mierle, G., and Ingram, R. 1991. The role of humic substances in the mobilization of mercury from watersheds. Water Air Soil Pollut. **56**: 349–357.

Moller, A.P., and Jennions, M.D. 2002. How much variance can be explained by ecologists and evolutionary biologists? Oecologia, **132**: 492–500.

Molot, L.A., and Dillon, P.J. 1997. Colour – mass balances and colour – dissolved organic carbon relationships in lakes and streams in central Ontario. Can. J. Fish. Aquat. Sci. **54**: 2789–2795.

Monson, B.A., and Brezonik, P.L. 1998. Seasonal patterns of mercury species in water and plankton from softwater lakes in northeastern Minnesota. Biogeochemistry, **40**: 147–162.

Monteiro, L.R., Isidro, E.J., and Lopes, H.D. 1991. Mercury content in relation to sex, size, age and growth in 2 scorpionfish (*Helicolenus dactylopterus* and *Pontinus kuhlii*) from Azorean waters. Water Air Soil Pollut. **56**: 359–367.

Morrison, K.A., and Watras, C.J. 1999. Mercury and methyl mercury in freshwater seston: direct determination at picogram per litre levels by dual filtration. Can. J. Fish. Aquat. Sci. **56**: 760–766.

Ontario Ministry of the Environment. 2003. Guide to eating Ontario sport fish. 2003–2004. Queen's Printer for Ontario, Toronto, Ontario.

Parkman, H., and Meili, M. 1993. Mercury in macroinvertebrates from Swedish forest lakes — influence of lake type, habitat, life-cycle, and food quality. Can. J. Fish. Aquat. Sci. **50**: 521–534.

Paterson, M.J., Rudd, J.W.M., and St. Louis, V. 1998. Increases in total and methylmercury in zooplankton following flooding of a peatland reservoir. Environ. Sci. Technol. **32**: 3868–3874.

Qian, S.S., Warren-Hicks, W., Keating, J., Moore, D.R.J., and Teed, R.S. 2001. A predictive model of mercury fish tissue concentrations for the southeastern United States. Environ. Sci. Technol. **35**: 941–947.

Rabenstein, D.L., and Fairhurst, M.T. 1975. Nuclear magnetic-resonance studies of solution chemistry of metal complexes. 11. Binding of methylmercury by sulfhydryl-containing amino-acids and by glutathione. J. Am. Chem. Soc. **97**: 2086–2092.

© 2005 NRC Canada

Rennie, M.D. 2003. Mercury in aquatic foodwebs: refining the use of mercury in energetics models of wild fish populations. M.Sc. thesis, University of Toronto, Toronto, Ont.

Rowan, D.J., and Rasmussen, J.B. 1994. Bioaccumulation of radiocesium by fish — the influence of physicochemical factors and trophic structure. Can. J. Fish. Aquat. Sci. **51**: 2388–2410.

Rudd, J.W.M. 1995. Sources of methyl mercury to fresh-water ecosystems — a review. Water Air Soil Pollut. **80**: 697–713.

SAS Institute Inc. 1989. SAS version 6.12 [computer program]. SAS Institute Inc., Cary, North Carolina.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practices of statistics in biological research. 3rd ed. W.H. Freeman and Company, New York.

Sonesten, L. 2001. Mercury content in roach (*Rutilus rutilus* L.) in circumneutral lakes — effects of catchment area and water chemistry. Environ. Pollut. **112**: 471–481.

Sonesten, L. 2003. Catchment area composition and water chemistry heavily affects mercury levels in perch (*Perca fluviatilis* L.) in circumneutral lakes. Water Air Soil Pollut. **144**: 117–139.

Suns, K., and Hitchin, G. 1990. Interrelationships between mercury levels in yearling yellow perch, fish condition and water-quality. Water Air Soil Pollut. **50**: 255–265.

Systat Software Inc. 1998. SYSTAT version 9 [computer program]. Systat Software Inc., Point Richmond, California.

Tremblay, A., and Lucotte, M. 1997. Accumulation of total mercury and methyl mercury in insect larvae of hydroelectric reservoirs. Can. J. Fish. Aquat. Sci. **54**: 832–841.

Tremblay, A., Lucotte, M., and Rowan, D.J. 1995. Different factors related to mercury concentration in sediments and zooplankton of 73 Canadian lakes. Water Air Soil Pollut. **80**: 961–970.

Tremblay, A., Lucotte, M., and Schetagne, R. 1998. Total mercury and methylmercury accumulation in zooplankton of hydroelectric reservoirs in northern Quebec (Canada). Sci. Total Environ. **213**: 307–315.

Trudel, M., and Rasmussen, J.B. 1997. Modeling the elimination of mercury by fish. Environ. Sci. Technol. **31**: 1716–1722.

US Environmental Protection Agency. 2002. Method 1631, revision E: mercury in water by oxidation, purge and trap, and cold vapor atomic fluorescence spectrometry. EPA-821-R-02-019, Office of Water, Washington, D.C.

Vander Zanden, M.J., and Rasmussen, J.B. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. Ecol. Monogr. **66**: 451–477.

Vander Zanden, M.J., and Vadeboncoeur, Y. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology, **83**: 2152–2161.

Visman, V., Mierle, G., and McQueen, D.J. 1995. Uptake of aqueous methylmercury by larval *Chaoborus americanus*. Water Air Soil Pollut. **80**: 1007–1010.

Watras, C.J., and Bloom, N.S. 1992. Mercury and methylmercury in individual zooplankton — implications for bioaccumulation. Limnol. Oceanogr. **37**: 1313–1318.

Watras, C.J., Bloom, N.S., Claas, S.A., Morrison, K.A., Gilmour, C.C., and Craig, S.R. 1995*a*. Methylmercury production in the anoxic hypolimnion of a dimictic seepage lake. Water Air Soil Pollut. **80**: 735–745.

Watras, C.J., Morrison, K.A., Host, J.S., and Bloom, N.S. 1995*b*. Concentration of mercury species in relationship to other site-specific factors in the surface waters of northern Wisconsin lakes. Limnol. Oceanogr. **40**: 556–565.

Westcott, K., and Kalff, J. 1996. Environmental factors affecting methyl mercury accumulation in zooplankton. Can. J. Fish. Aquat. Sci. **53**: 2221–2228.

Wren, C.D., and Stephenson, G.L. 1991. The effect of acidification on the accumulation and toxicity of metals to fresh-water invertebrates. Environ. Pollut. **71**: 205–241.

Xun, L., Campbell, N.E.R., and Rudd, J.W.M. 1987. Measurements of specific rates of net methyl mercury production in the water column and surface sediments of acidified and circumneutral lakes. Can. J. Fish. Aquat. Sci. **44**: 750–757.

Appendix A

Table A1. Averages of environmental characteristics for 23 water bodies under study and number of observations from each lake included in cross-validated data sets.

Water body	Water-body code[a]	Location[b]	pH	[DOC] ($mg \cdot L^{-1}$)	No. of observations in expanded data set
D24N (north basin)	R	1	6.37	10.68	8
D24S (south basin)	R	1	6.21	10.74	7
Detcheverry	L	1	6.97	8.88	3
Des Voeux	L	1	6.90	5.52	5
Duncan	L	1	6.55	9.05	8
km 17	R	1	7.36	7.28	3
Laporte	L	1	6.30	8.49	1
Evans	L	1	6.85	10.46	1
Jobert	L	1	6.80	6.30	1
Koury	L	1	6.40	8.27	1
LA40	R	1	5.84	7.80	7
Opinaca	L	1	6.24	10.36	1
Plastic	L	2	5.57	2.05	4
Shoe	L	2	6.62	3.24	4
Ashley	L	2	6.7	8.2	1
Lady Ruth	L	2	6.5	8.4	1
Margueratt	L	2	6.8	8.5	1

© 2005 NRC Canada

Table A1 (*concluded*).

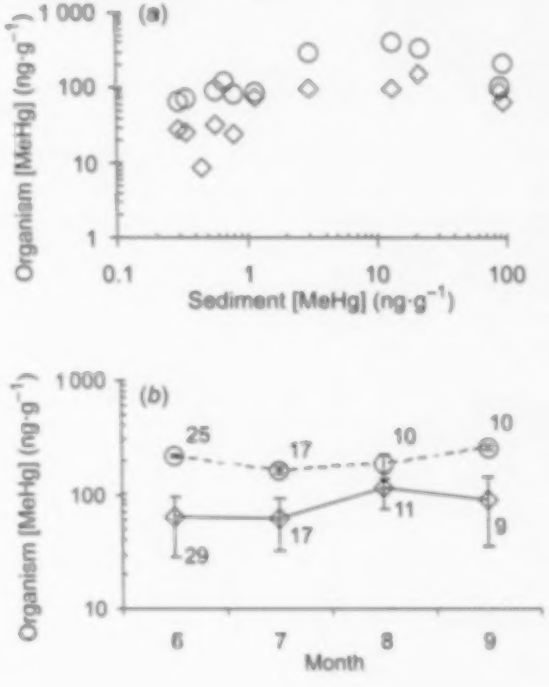
Water body	Water-body code[a]	Location[b]	pH	[DOC] (mg·L^{-1})	No. of observations in expanded data set
Melick	L	2	7.3	9.0	1
Trailer	L	2	7.4	9.0	1
L240	L	3	7.17	6.69	2
L632	L	3	5.79	13.20	3
L979	L	3	6.66	9.34	2
L979R (postflooding)	R	3	6.29	13.94	4

[a]R, reservoir; L, lake.
[b]1, northwestern Quebec; 2, north-central Ontario; 3, northwestern Ontario.

Appendix B

We evaluated relationships between organism [MeHg] with sediment [MeHg] and the season in which organisms were collected. Correlations between collector–shredder [MeHg] and sediment [MeHg] were strong and significant (Pearson $r = 0.72$, $p = 0.012$, $p_{crit} = 0.025$). Correlatons between predator [MeHg] and sediment [MeHg] were similar but insignificant after Bonferroni correction (Pearson $r = 0.63$, $p = 0.038$, $p_{crit} = 0.025$). However, patterns of sediment [MeHg] with [MeHg] for both functional groups were largely similar over the range of variation observed (Fig. B1*a*). We also performed a three-factor ANOVA on organism [MeHg] treating functional group and month as fixed factors and lake as a randomized block factor. Removing the effect of lake, the month of collection did not explain a significant component of variation in organism [MeHg] ($F_{[3,98]} = 0.49$, $p = 0.69$), and there was no significant interaction between functional group and month ($F_{[3,98]} = 0.27$, $p = 0.27$) (Fig. B1*b*). This supports insignificant findings of single-factor ANOVAs performed on the month of collection for each functional group [MeHg], disregarding potential lake effects (ANOVA: predators, $F_{[3,62]} = 1.05$, $p = 0.38$; collectors–shredders, $F_{[3,58]} = 0.92$, $p = 0.43$).

Fig. B1. Relationships of organism [MeHg] with (*a*) sediment [MeHg] and (*b*) month of invertebrate collection, variables not considered in empirical models. Circles, predators; diamonds, collectors–shredders. In *b*, error bars are ±1 SE, and the numbers beside each data point represent the number of individuals used to generate means and standard errors.



© 2005 NRC Canada

An experimental evaluation of competitive and thermal effects on brown trout (*Salmo trutta*) and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) performance along an altitudinal gradient

Peter McHugh and Phaedra Budy

Abstract: Temperature-mediated competition (i.e., dominance shifts between species depending on temperature) may explain the segregation of salmonid species along altitudinal stream gradients. We evaluated this hypothesis for exotic brown trout (*Salmo trutta*) and native Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) by rearing them in experimental sympatry and allopatry using enclosures constructed at six sites spaced along a 45-km segment of a mountain stream. For both species, we compared condition and growth between allopatric and sympatric treatment groups. We found that brown trout negatively affected cutthroat trout performance, whereas cutthroat trout failed to impart an effect in the reverse direction, regardless of temperature. Thus, we documented asymmetric competition between these species but found little evidence indicating that its outcome was influenced by temperature. Brown trout – cutthroat trout segregation is therefore unlikely to be due to temperature-mediated competition. Instead, brown trout may have displaced cutthroat trout from downstream areas through competition or other mechanisms, while abiotic factors preclude their (brown trout) invasion of upper elevations. Given the magnitude of effect observed in our study, we recommend that brown trout receive greater consideration in cutthroat trout conservation.

Résumé : La compétition reliée à la température, dans laquelle la dominance passe d'une espèce à une autre en fonction de la température, peut probablement expliquer la ségrégation des espèces de salmonidés le long de gradients d'altitude dans les cours d'eau. Nous avons éprouvé cette hypothèse chez des truites brunes (*Salmo trutta*) exotiques et des truites fardées Bonneville (*Oncorhynchus clarkii utah*) indigènes en les élevant ensemble (sympatrie expérimentale) ou séparément (allopatrie) dans des enclos construits à six sites échelonnés sur un segment de 45 km d'un cours d'eau de montagne. Chez les deux espèces, nous avons comparé la condition et la croissance des groupes de poissons élevés dans des conditions de sympatrie et d'allopatrie. La truite brune affecte négativement la performance de la truite fardée, alors que la truite fardée n'arrive pas à avoir d'impact sur la truite brune, quelle que soit la température. Il y a donc une compétition asymétrique entre ces deux espèces, mais il y a peu d'indications que l'issue de la compétition est influencée par la température. La ségrégation entre la truite brune et la truite fardée n'est vraisemblablement pas due à la compétition reliée à la température. Il est possible que la truite brune élimine la truite fardée des zones d'aval par compétition ou par un autre mécanisme, alors que les facteurs abiotiques empêchent l'invasion des altitudes plus élevées par la truite brune. Étant donné l'ampleur des effets observés dans notre étude, nous recommandons de porter plus d'attention à la truite brune dans les travaux de conservation de la truite fardée.

[Traduit par la Rédaction]

Introduction

Patterns of fish-species replacement along altitudinal gradients occur commonly in mountain rivers and streams throughout the world (Taniguchi and Nakano 2000). This phenomenon — termed altitudinal species zonation because of the distinct species zones observed along upstream–downstream gradients — occurs in response to factors operating differentially across elevations. Zonation may be due to the response of individual species to the availability of suitable habitat conditions that vary with elevation (e.g., temperature; Vincent and Miller 1969; Rahel and Hubert 1991; Bozek and Hubert 1992). For instance, each species may have a different thermal physiology and thus exhibit a distribution pattern reflecting the spatial arrangement of suitable temperatures within a river network (Magoulick and Wilzbach 1998*a*).

More locally, species-zonation patterns can be the result of an interaction between abiotic and biotic factors (Dunson and Travis 1991; Fausch et al. 1994). For example, temperature-

Received 29 December 2004. Accepted 4 July 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 29 October 2005.
J18484

P. McHugh[1] and P. Budy. US Geological Survey – Utah Cooperative Fish and Wildlife Research Unit, Department of Aquatic, Watershed, and Earth Resources, College of Natural Resources, Utah State University, Logan, UT 84322-5210, USA.

[1]Corresponding author (e-mail: pam@cc.usu.edu).

 doi: 10.1139/F05-184 © 2005 NRC Canada

mediated competition may be the reason why salmonid species segregate along altitudinal gradients (Fausch 1989; Fausch et al. 1994; de la Hoz Franco and Budy 2005). Under this scenario, high-elevation species are hypothesized to be superior competitors at cold temperatures and to exclude low-elevation species from areas dominated by those conditions, while the reverse is thought to be true at low-elevation, warmer sites. In the absence of the competitor(s), each species may be physiologically capable of living at all sites (Taniguchi and Nakano 2000). While there have been several recent experiments designed to evaluate temperature-mediated competition as an explanation for salmonid zonation (see Discussion for a review of these studies), results have been variable (Novinger 2000; De Staso and Rahel 1994).

Because of the threatened and endangered status of many native fishes, it is imperative to understand the influence of temperature-mediated competition on salmonid zonation in streams. Non-native trout invasions are perceived as one of the greatest threats to native salmonid diversity in North America (Dunham et al. 2002; Quist and Hubert 2004). In many watersheds of the western US and Canada, native cutthroat trout (*Oncorhynchus clarkii* subsp.) persist only in headwater reaches, while non-native brook (*Salvelinus fontinalis*) and exotic brown trout (*Salmo trutta*) replace them at lower elevations (Fausch 1989; de la Hoz Franco and Budy 2005). Given the imperiled status of cutthroat trout (Gresswell 1988; Behnke 1992; Young 1995), identifying the causes of zonation in native–non-native trout systems is of considerable importance. Specifically, understanding whether cutthroat trout distributional limits are set by abiotic conditions, competition with exotic species, or an interaction between the two will lead to different strategies when attempting to increase the size and spatial extent of cutthroat trout populations, a goal common to recovery plans (e.g., Lentsch et al. 1997).

In this study, we evaluated the causes of spatial segregation between exotic brown trout and native Bonneville cutthroat trout (*O. c. utah*) in a stream in northern Utah, USA. Native to the ancient Lake Bonneville Basin of the USDA Forest Service Intermountain Region, Bonneville cutthroat trout are only present in a fraction of their historic range and are being considered for US Endangered Species Act protection (Duff 1988; Young 1995; Lentsch et al. 1997). In contrast, brown trout (a species native to Europe and Asia) are widely distributed in the region and abundant in many streams that were historically dominated by cutthroat trout. When they co-occur, brown trout and cutthroat trout segregate along altitudinal gradients (de la Hoz Franco and Budy 2005). To understand this pattern, we experimentally assessed the interacting roles of interspecific competition and water temperature on brown and cutthroat trout performance in a field setting.

Materials and methods

Study site description

We conducted our experiment within a 45-km segment of the Logan River, Utah, USA, a stream that originates in the Bear River Mountain Range of northern Utah and drains into the terminal Great Salt Lake system (Fig. 1). This mountain stream of moderate elevation (study reach range: 1503–2091 m) and gradient (0.015 $m \cdot m^{-1}$) flows through a broad valley in its upper reaches and a deeply dissected canyon in its lower reaches. The climate of the area is characterized by cold, snowy winters (January air temperature: low, –9 °C; high, 0 °C; mean precipitation 4.0 cm) and hot, dry summers (July air temperature: low, 15 °C; high, 31 °C; mean precipitation 1.6 cm), yielding a hydrograph dominated by a spring-snowmelt flood (554 $ft^3 \cdot s^{-1}$; 1 cubic foot per second = 28.316 $dm \cdot s^{-1}$) followed by base-flow conditions (~100 $ft^3 \cdot s^{-1}$).

In addition to Bonneville cutthroat trout, the species of primary interest in our study, other native fishes present in the Logan River include mottled sculpin (*Cottus bairdii*) and mountain whitefish (*Prosopium williamsoni*). Introduced species include brown trout, with rainbow (*Oncorhynchus mykiss*) and brook trout also present but in low numbers. Species abundance varies with elevation in the Logan River, producing three fish zones (de la Hoz Franco and Budy 2005): (*i*) a low-elevation zone dominated by brown trout; (*ii*) a high-elevation zone dominated by cutthroat trout; and (*iii*) a mid-elevation transitional area (Fig. 2).

Experimental design

We evaluated the influence of competition and temperature on brown trout – cutthroat trout zonation. An enclosure experiment was set up where these species were reared together (in sympatry) and alone (in allopatry) at six points systematically spaced along the thermal gradient present in the Logan River. The spatial aspect of our design thus incorporated the natural temperature range and the three fish zones of the Logan River, allowing us to simultaneously assess the role of temperature and competitive interactions in zonation. We did this using a substitutive competition experiment (sensu Fausch 1998) within the context of a randomized complete block design. At each site, we constructed three 20-m^2 rectangular enclosures (6.0 m × 3.3 m, long sides parallel to flow) from steel T-posts and 13-mm plastic mesh. Enclosures were arranged within sites so that one side was attached to the riverbank. Also, there was at least 10 m of free-flowing river between enclosures at sites where they were built in an upstream–downstream sequence. We randomly assigned treatments to enclosures within sites. The treatment levels were (*i*) eight cutthroat trout in allopatry, (*ii*) eight brown trout in allopatry, and (*iii*) four brown and four cutthroat trout in sympatry. The density of experimental fish in enclosures (0.40 fish·m^{-2}) reflects the upper limit of densities observed for trout in the Logan River (Budy et al. 2004).

Trout used in the experiment were collected from allopatric locations within the study watershed (brown trout from Right Hand Fork; cutthroat trout from Beaver Creek and the Logan River at Franklin Basin; Fig. 1) using backpack electrofishing methods. Brown trout (mean total length (TL): 180 mm, 95% confidence interval (CI): 175–185 mm) and cutthroat trout (mean TL: 173 mm, 95% CI: 167–178 mm) used in our experiment were of similar starting TL; however, because of the natural size structure present in the Logan River, experimental brown trout were slightly longer than experimental cutthroat trout. Upon collection, we transported all fish to laboratory raceways and held them at 10 °C for an 8-day acclimation period to ensure that all fish had the same recent thermal history prior to exposure to experi-

© 2005 NRC Canada

Fig. 1. Map of the Logan River Drainage in northern Utah, USA. The experimental reach extends from the Idaho border (northern edge of detailed figure) to the lower end of US Forest Service ownership (at the city boundary). Enclosure sites are labeled with shaded symbols and site name. Experimental fish were collected from Right Hand Fork, Beaver Creek, and the mainstem Logan River upstream of the Franklin Basin site.

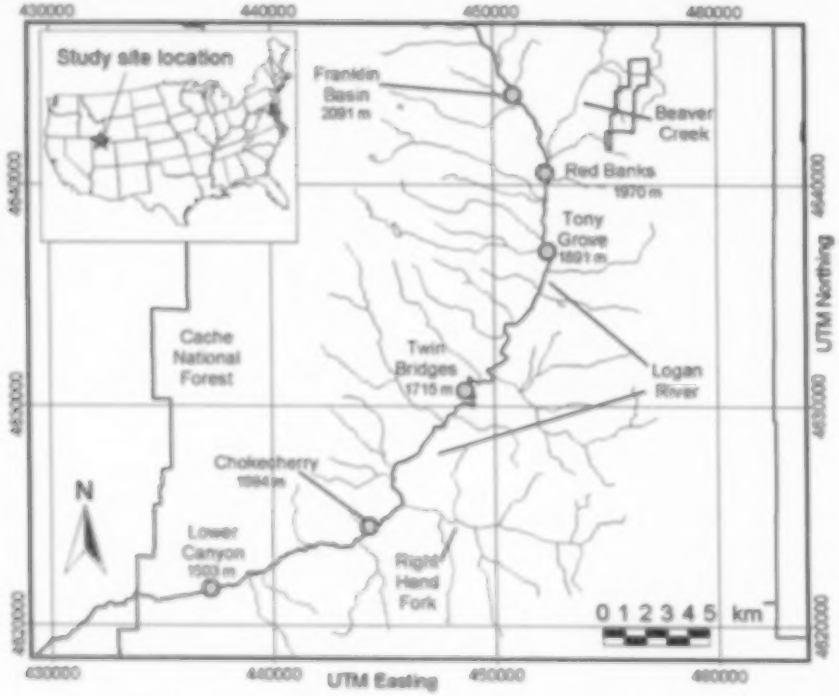
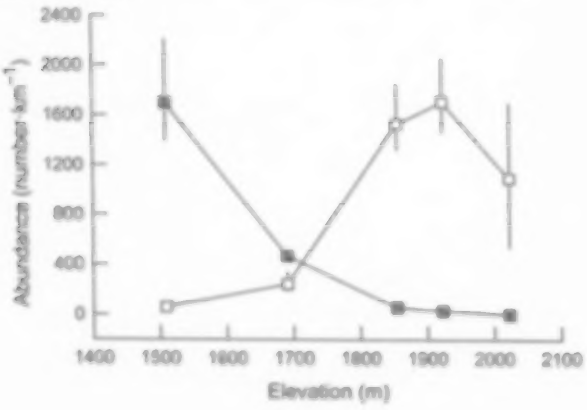


Fig. 2. The brown trout (*Salmo trutta*; shaded symbols) – Bonneville cutthroat trout (*Oncorhynchus clarkii utah*; open symbols) altitudinal species-zonation pattern of Logan River, Utah. Estimates of trout abundance are from Budy et al. (2004) and represent the mean (± range) based on three-pass electrofishing surveys made at five long-term monitoring sites in the summers of 2001–2003.



mental temperatures. During this period, fish were starved, weighed, measured, and given a uniquely numbered T-bar anchor tag.

Individual fish were randomly assigned to each site–treatment combination and introduced into enclosures simultaneously on 14 July 2003 to begin a 42-day trial. During this period, fish were assumed to have sufficient prey resources (e.g., terrestrial, benthic, and (or) drifting macroinvertebrates); a pilot study indicated that when enclosure mesh was cleaned of debris, invertebrate drift was unimpeded. We cleaned all enclosures at least once every 48 h during the trial period to provide a regular supply of prey. Other than routine cleaning visits, we allowed fish to interact with minimal disturbance during the experiment. On 25 August 2003, the experiment was concluded, and all fish were collected from enclosures (using electrofishing and underwater collection methods), weighed, and measured. As a rule, we included in our analysis only those enclosures that contained at least five of the eight experimental fish and at least two of each species (for sympatric replicates only). For both species, this resulted in five and six replicates for sympatric and allopatric treatment groups, respectively.

Fish performance

We evaluated the performance response of brown and cutthroat trout to species interactions and abiotic conditions based on two measures. First, we assessed their instantaneous (specific) growth rate, G:

$$(1) \qquad G = [(\ln W_{final} - \ln W_{initial}) \times t^{-1}] \times 100$$

© 2005 NRC Canada

Table 1. Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) and brown trout (*Salmo trutta*) initial total length (TL), release, recapture, and tag retention details by site and treatment.

		Cutthroat trout				Brown trout			
Site	Treatment	TL (mm)	Release (*n*)	Recapture (*n*)	w/tag	TL (mm)	Release (*n*)	Recapture (*n*)	w/tag
Lower Canyon	Allopatry	177	8	7	5	185	8	7	7
	Sympatry	176	4	4	4	194	4	4	4
Chokecherry	Allopatry	165	8	7	5	188	8	7	7
	Sympatry	168	4	2	0	179	4	3	3
Twin Bridges	Allopatry	179	8	5	5	181	8	8	6
	Sympatry[a]	169	4	2	2	170	4	1	1
Tony Grove	Allopatry	178	8	7	5	172	8	6	5
	Sympatry	171	4	3	1	166	4	4	4
Red Banks	Allopatry	165	8	7	7	171	8	7	7
	Sympatry	174	4	4	4	170	4	3	3
Franklin Basin	Allopatry	176	8	7	7	187	8	8	8
	Sympatry	177	4	3	3	193	4	4	4

Note: The category "w/tag" denotes the number of fish recaptured that retained their tag. The total density of fish in sympatric enclosures is the sum of brown and cutthroat trout released (i.e., 8).

[a]This enclosure was omitted from our analysis because of fish losses.

where W is mass in grams and t is trial length in days. Owing to high tag loss rates (Table 1) and the disappearance of some fish, however, we were unable to definitively identify every individual on several instances. Thus, we evaluated growth rates using enclosure-averaged start ($W_{initial}$) and end (W_{final}) weights.

In addition to growth, we assessed the condition of individual fish based on the relative weight index, W_r:

$$(2) \qquad W_r = W/W_s \times 100$$

where W is the observed mass (g) of a given fish, and W_s is its predicted mass (g) based on its measured total length (mm) and a standard length–weight relationship for the species. Our standard length–weight relationships were those estimated for wild, Logan River brown and cutthroat trout sampled during annual monitoring activities (brown trout, $W_s = 1.708 \times 10^{-5}$ TL$^{2.905}$; cutthroat trout $W_s = 6.193 \times 10^{-5}$ TL$^{2.670}$; Budy et al. 2004). Pretrial condition values were similar for fish assigned to the two treatment groups for both species (analysis of variance: brown trout, $F_{[1,9]} = 1.5$, $P = 0.256$; cutthroat trout, $F_{[1,9]} = 0.1$, $P = 0.834$), indicating that any differences observed at the end of the trial are due to experimental effects. Finally, although quantifying behavioral performance would have been desirable, preliminary underwater and aerial observations demonstrated that encounter rates were insufficient to warrant such an assessment.

Environmental variable measurement

To evaluate the effects of environmental factors on performance and competitive relationships and to account for cage effects in our analysis, we quantified several habitat characteristics at both the site and enclosure levels. Water temperature, the site-level variable of primary interest in our study, was measured hourly using data loggers. From these data, we computed the daily mean, minimum, and maximum temperature for the 42-day period. We also quantified stream size at the site level using a single, base-flow, discharge measurement made with an electromagnetic flow meter.

In addition to taking site-level environmental measurements, we assessed habitat within individual enclosures. First, we measured the size distribution of streambed particles using a Wolman pebble count (Wolman 1954), which was summarized by the median particle size (D_{50}). To account for fine sediment deposition caused by velocity differences between the inside and outside of enclosures and due to changes in flow across the 42-day period, we estimated the percentage of the enclosed area covered by fines (<10 mm) visually at the beginning and end of the trial. We also estimated the mean depth (cm) and velocity (cm·s^{-1}) based on measurements made at 20 evenly spaced points in a grid spanning each enclosure. Finally, we quantified prey abundance based on the assumption that the area upstream of enclosures was the main source of drifting invertebrates during the experiment. Thus, we collected three benthic invertebrate samples ~2 m upstream of each enclosure using a 0.09-m^2 Surber sampler. Samples were preserved (95% ethanol) and transported to the laboratory, where invertebrates were counted and identified (to Order) using a dissecting microscope. We measured the length of 30 individuals and estimated dry biomass based on length–mass regressions (Benke et al. 1999) for the Orders Ephemeroptera, Plecoptera, Diptera, and Trichoptera; for a given enclosure, we averaged the three samples.

Statistical analysis

Our analysis occurred in two phases. First, we compared the upstream–downstream temperature profile measured during our experiment to literature-based, thermal physiology criteria for each species, without any consideration of trial results. We contrasted minimum, mean, and maximum water temperatures from the six sites with the thermal growth optima of brown trout (13–18 °C; Elliott and Hurley 2000; Ojanguren et al. 2001) and cutthroat trout (13–19 °C; based on the optimum growth temperature – lethal temperature relationship of Jobling (1981) and also on the published thermal physiology data for Bonneville cutthroat trout (Wagner

© 2005 NRC Canada

et al. 2001; Johnstone and Rahel 2003)). Additionally, we evaluated brown trout growth potential across the six sites using the temperature–growth model of Elliott et al. (1995). This model, based on growth experiments where brown trout were fed maximum ration at several temperatures, predicts growth based on a fish's initial mass ($W_{initial}$ in eq. 1 above), trial duration, mean water temperature, and three parameters. No such model has been developed for Bonneville cutthroat trout (or related subspecies), so we completed this analysis component for brown trout only.

For the second phase of our analysis, we compared the condition and growth of experimental fish separately, between treatment groups, and within species as a function of temperature using analysis of covariance (ANCOVA). Because we were mainly interested in assessing how temperature extremes affect the outcome of competition, we used two temperature metrics (minimum and maximum) in separate analyses. However, based on the potential for site effects due to factors other than temperature (e.g., food availability), we also considered a subset of non-temperature environmental variables (i.e., discharge, end fines, D_{50}, and prey biomass; all uncorrelated with temperature ($|R| < 0.5$) based on an initial screening of Pearson's correlation coefficients). The model structure used was

$$(3) \qquad y_{ij} = \mu + \mathrm{trt}_i + \beta_1 X_{1ij} + \beta_{2i} T_{ij} + \varepsilon_{ij}$$

where y_{ij} is the performance observed in the jth enclosure within the ith treatment group, μ is an intercept term, trt_i is an effect due to the ith treatment, $\beta_1 X_{1ij}$ is a non-temperature site effect, $\beta_{2i} T_{ij}$ is the treatment-specific effect of temperature (i.e., inclusive of a temperature-by-treatment interaction), and ε_{ij} is the residual error term.

Prior to fitting the final ANCOVA model and evaluating experimental effects, we used a model selection strategy based on Akaike's Information Criterion (AIC_c, adjusted for small sample size) (Burnham and Anderson 2002) to identify which environmental variable best accounted for non-temperature site effects (i.e., $\beta_1 X_{1ij}$). We then fit the best model and assessed model-effect significance using F tests (Type III sums of squares). Finally, we compared ANCOVA-adjusted mean performance (condition and growth) between treatment groups in a post hoc context using t tests for both. Post hoc comparisons were completed for both high and low temperature levels when there was a significant treatment–temperature interaction and at average covariate values otherwise. Model-selection analyses were completed using SAS's PROC REG, whereas the final ANCOVA models were completed using PROC GLM (SAS Institute Inc. 2002). Owing to the low replication and high variability of our data set, we assessed significance at $\alpha = 0.10$.

Results

Longitudinal temperature profile

In general, water temperatures measured during the experiment decreased with increasing elevation across the study reach (Table 2). Mean and maximum temperatures increased across the three upper-most sites (Franklin Basin to Tony Grove) and then remained relatively constant in the downstream direction; minimum temperature increased as a nearly linear, inverse function of elevation. The greatest diel fluctuation (maximum – minimum temperature) was observed at a mid-elevation site (Tony Grove).

Based on published thermal physiology information for brown and cutthroat trout (see Materials and methods), it appears that both species experienced optimum growth temperatures during part of every day at all sites, excluding the uppermost site (Franklin Basin). Using observed mean temperatures and starting weights, the model of Elliott et al. (1995) predicted that brown trout growth rates should be highest at mid-elevation sites (Twin Bridges: 0.766 day^{-1}, and Tony Grove: 0.798 day^{-1}), lowest at high elevation sites (Red Banks: 0.542 day^{-1}, and Franklin Basin: 0.362 day^{-1}), and intermediate at the two lowermost sites (Lower Canyon: 0.656 day^{-1}, and Chokecherry: 0.715 day^{-1}).

Experimental effects of temperature and competition on trout

On average, seven of the eight experimental fish were recaptured in enclosures. Only one replicate (i.e., a site–treatment combination) had to be withheld from analysis (Twin Bridges-sympatric) because of fish losses ($n = 3$ fish remained; Table 1). Documented fish losses were due to predation by birds (P. McHugh, personal observation); however, losses occurred because of unknown causes as well.

Both trout species exhibited positive growth and relatively high condition across the six sites. Thus, there was not a clear trend in performance along the thermal gradient of the study site for either species. Overall, brown and cutthroat trout growth rates averaged 0.904 day^{-1} (range: 0.219–1.604 day^{-1}) and 0.384 day^{-1} (range: 0.039–0.930 day^{-1}), respectively. Brown trout weight was similar to that of non-experimental Logan River fish of the same size, with an overall mean relative weight (condition) of 100.2% (range: 79.7%–119.1%). In contrast, cutthroat trout weighed less than the standard weight equation predicted, attaining a mean condition value of 83.7% (range: 63.5%–106.0%). Brown trout growth and condition were higher in sympatric compared with allopatric enclosures (Figs. 3*a* and 3*b*). In contrast, cutthroat trout performance was suppressed in sympatry relative to allopatry (Figs. 3*c* and 3*d*).

Our evaluation of the effects of species interactions and abiotic factors on experimental trout performance illustrates three important results. First, site-level differences in non-temperature environmental factors (discharge or prey biomass, selected using AIC_c) accounted for a large proportion of variability in trout performance. Second, cutthroat trout presence, water temperature, or their interaction did not have a demonstrable effect on brown trout condition or growth (Table 3; Fig. 3). In fact, post hoc comparisons of ANCOVA-adjusted means indicate that brown trout attained significantly higher condition values in the presence of cutthroat trout (minimum temperature–condition, $t = -4.45$, df = 6, $P = 0.004$; maximum temperature-condition, $t = -3.56$, df = 6, $P = 0.0119$). Brown trout growth differences, though in agreement with the trend in condition between treatment groups, were negligible (see Table 3 for ANCOVA results; post hoc means comparisons: minimum temperature–growth, $t = -0.56$, df = 6, $P = 0.594$; maximum temperature–growth, $t = -0.58$, df = 6, $P = 0.586$). Thus, there was an overall lack of statistical support for a negative competitive effect — temperature mediated or otherwise — of cutthroat trout on brown trout.

© 2005 NRC Canada

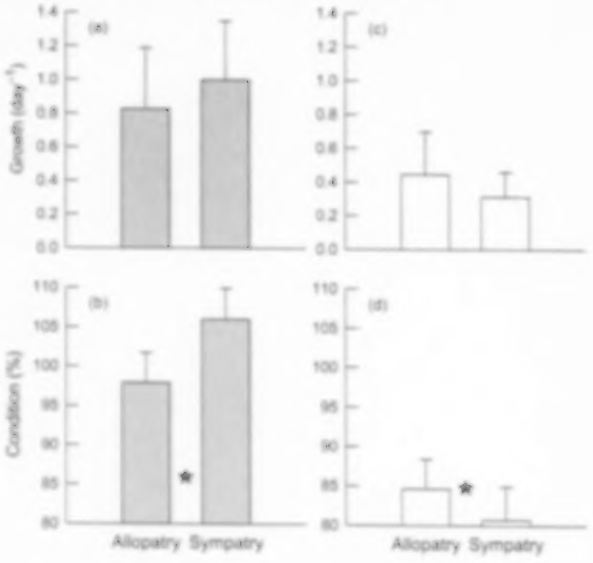
Table 2. Site-level and enclosure-level habitat attributes of experimental enclosures.

		Site-level attributes					Enclosure-level attributes					
			Temperature (°C)									
Site	Treatment	Elevation (m)	Mean	Min.	Max.	Discharge (cfs)	Depth (cm)	Velocity ($cm \cdot s^{-1}$)	Start fines (%)	End fines (%)	D_{50} (mm)	Prey biomass ($mg \cdot m^{-2}$)
Lower Canyon	CUT	1503	13.9	11.8	16.2	32	33	18	6	45	34	5 056
	BNT	—	—	—	—	—	32	32	0	3	90	12 444
	BNT+CUT	—	—	—	—	—	29	25	0	3	60	12 778
Chokecherry	CUT	1564	12.5	10.4	14.8	95	41	16	56	79	12	3 489
	BNT	—	—	—	—	—	34	23	33	74	4	3 178
	BNT+CUT	—	—	—	—	—	33	25	0	43	45	3 800
Twin Bridges	CUT	1715	13.1	10.1	16.0	70	44	17	50	88	4	2 978
	BNT	—	—	—	—	—	33	21	22	73	4	3 600
	BNT+CUT	—	—	—	—	—	28	20	22	45	12	5 033
Tony Grove	CUT	1891	12.9	8.9	17.5	36	26	22	0	45	50	4 367
	BNT	—	—	—	—	—	36	8	22	58	25	2 100
	BNT+CUT	—	—	—	—	—	31	21	11	33	62	3 389
Red Banks	CUT	1970	9.9	6.9	13.8	37	42	32	0	5	112	7 200
	BNT	—	—	—	—	—	30	29	0	30	45	4 722
	BNT+CUT	—	—	—	—	—	34	36	6	5	85	6 756
Franklin Basin	CUT	2091	8.1	6.1	11.2	16	44	22	0	35	95	5 133
	BNT	—	—	—	—	—	27	17	0	28	75	5 833
	BNT+CUT	—	—	—	—	—	26	21	13	42	21	3 889

Note: BNT, brown trout (*Salmo trutta*); CUT, Bonneville cutthroat trout (*Oncorhynchus clarkii utah*); —, value applies to all enclosures at that particular site; cfs, cubic feet per second (1 cubic foot per second = 28.316 $dm \cdot s^{-1}$); D_{50}, median particle size. See text for measurement and computation details.

© 2005 NRC Canada

Fig. 3. Mean growth and condition (±2 SE) for brown trout (*Salmo trutta*; panels *a* and *b*, shaded bars) and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*; panels *c* and *d*, open bars) raised in sympatry and allopatry. An asterisk denotes a statistically significant difference ($\alpha = 0.10$) between treatment group means adjusted by analysis of covariance.



In contrast with our brown trout results, our analysis provided statistical evidence for a negative competitive impact of brown trout on cutthroat trout (Fig. 3). First, treatment and temperature–treatment interaction effects were both significant in the cutthroat trout maximum temperature–condition model (Table 4). Specifically, allopatric cutthroat trout attained a condition value nearly 10% greater than did cutthroat trout reared with brown trout at a maximum temperature of 12 °C (post hoc means comparison: $t = 3.3$, df = 6, $P = 0.016$). Condition was only 2% higher among allopatric relative to sympatric fish at 17 °C ($t = 0.47$, df = 6, $P = 0.655$). In contrast with maximum temperature–condition ANCOVA results, treatment and temperature–treatment interaction effects were not significant in all other models. However, a ANCOVA-adjusted mean comparison based on the minimum temperature–condition model corroborate the maximum temperature–condition findings ($t = 2.41$, df = 6, $P = 0.053$). Finally, although cutthroat trout growth was greater in allopatry relative to sympatry, ANCOVA-adjusted means did not differ significantly between treatment groups for either model ($P > 0.25$).

To summarize, brown trout greatly reduced cutthroat trout performance at all but the warmest of temperatures observed in our experiment. Experimental brown trout performance, in contrast, was generally unaffected by temperature and (or) competition with cutthroat trout.

Discussion

A central tenet of stream ecology is that abiotic conditions and biological communities change predictably along longitudinal (upstream–downstream) gradients (Vannote et al. 1980). This is particularly true for salmonids in stream environments, where species segregate into discrete zones and water temperatures change over relatively short distances (e.g., Vincent and Miller 1969). These systems are thus ideal for assessing the interacting roles of biotic interactions and abiotic factors in determining species distributions. Accordingly, we evaluated the potentially interacting roles of interspecific competition and temperature on the performance of two trout species in an effort to understand the causes of salmonid zonation.

If temperature-mediated competition were the ultimate cause of zonation in our study system, we would expect brown trout to negatively impact cutthroat trout at warm temperatures and cutthroat trout to similarly affect brown trout at cool temperatures. Counter to this prediction, however, brown trout presence reduced cutthroat trout performance at all but the warmest temperatures. Thus, while we present evidence of a negative effect of exotic brown trout on native cutthroat trout, temperature-mediated competition does not satisfactorily explain zonation in our system. Rather, we suggest that altitudinal segregation is due to an abiotic determination of brown trout's upstream limit, coupled with their demonstrated ability to negatively impact cutthroat trout when they co-occur. Specifically, we believe that brown trout have invaded as far upstream as their thermal physiology permits and during this process have displaced cutthroat trout from downstream reaches.

The role of temperature in zonation

Although temperature requirements of Bonneville cutthroat trout have not been fully quantified to date, a simultaneous consideration of their estimated growth optimum (13–19 °C; see Materials and methods for derivation details), the thermal gradient of the Logan River, and experimental fish performance indicates that temperature conditions do not adequately explain their absence from downstream reaches. Even the warmest, low-elevation conditions observed in our study (maximum temperature, 15–18 °C) were well within the derived optimum temperature range. Indeed, some of the highest growth and condition values were documented among allopatric cutthroat trout at our lowermost site. This result is corroborated by a number of recent studies demonstrating that Bonneville cutthroat trout are well adapted to survive and grow at temperatures well in excess of 20 °C (Wagner et al. 1998; Johnstone and Rahel 2003; Schrank et al. 2003). Thus, it is unlikely that warm water temperatures prevent cutthroat trout from occupying low-elevation sites.

Despite the absence of a clear performance–temperature trend for experimental brown trout, existing information suggests that cold temperatures preclude them from high-elevation reaches. First, though altitudinal trends in temperature and predicted growth potential (Elliott et al. 1995) indicate that positive brown trout growth is possible throughout our study river, the lowest predicted rate was for our coldest, highest site (0.361 day^{-1}, Franklin Basin). This site averaged only 8.1 °C (range: 6.1–11.2 °C), whereas brown trout optimum growth occurs between 13 and 18 °C (Elliott and Hurley 2000; Ojanguren et al. 2001). Thus, temperatures at high elevations are less than ideal — though not necessarily unsuitable — for subadult brown trout growth. Abiotic controls on brown

© 2005 NRC Canada

Table 3. Brown trout (*Salmo trutta*) analysis of covariance (ANCOVA) results results by temperature metric (minimum, T_{min}; maximum, T_{max}) and response variable (condition or specific growth rate).

		Condition (% relative weight)			Specific growth rate (day^{-1})		
Temperature model	Effect	R^2	$F_{[1,6]}$	P	R^2	$F_{[1,6]}$	P
Minimum	Treatment	0.89	0.9	0.392	0.45	0.0	0.883
	Site		**16.9**	**0.006**		1.6	0.258
	T_{min}		**12.1**	**0.013**		0.7	0.450
	T_{min}×Treatment		0.01	0.937		0.1	0.784
Maximum	Treatment	0.80	1.4	0.280	0.42	0.0	0.863
	Site		**8.2**	**0.029**		**3.9**	**0.096**
	T_{max}		0.2	0.716		0.4	0.538
	T_{max}×Treatment		0.5	0.514		0.0	0.923

Note: Bold F statistics and P values denote effect significant ($\alpha = 0.10$) in ANCOVA models. "Site" is the covariate discharge in both growth models and the minimum temperature–condition model; it is invertebrate biomass for the maximum temperature–growth model.

Table 4. Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) analysis of covariance (ANCOVA) results by temperature metric (minimum, T_{min}; maximum, T_{max}) and response variable (condition or specific growth rate).

		Condition (% relative weight)			Specific growth rate (day^{-1})		
Temperature model	Effect	R^2	$F_{[1,6]}$	P	R^2	$F_{[1,6]}$	P
Minimum	Treatment	0.76	1.7	0.243	0.52	1.4	0.287
	Site		**13.4**	**0.011**		2.1	0.199
	T_{min}		1.4	0.287		0.0	0.928
	T_{min}×Treatment		0.6	0.470		0.9	0.384
Maximum	Treatment	0.83	**5.8**	**0.054**	0.55	1.6	0.259
	Site		**17.4**	**0.006**		3.6	0.106
	T_{max}		0.8	0.412		0.3	0.610
	T_{max}×Treatment		**4.1**	**0.090**		1.2	0.319

Note: Bold F statistics and P values denote effect significant ($\alpha = 0.10$) in ANCOVA models. "Site" is the covariate discharge for condition analyses and invertebrate biomass for growth analyses.

trout distribution, however, may more strongly affect other, more sensitive life stages (e.g., embryos; see below).

We hypothesize that ultimately, the limiting effect of cold temperatures on brown trout occurs during a life stage prior to the one used in our experiment. First, it is clear that subadult and adult brown trout can access (Budy et al. 2004) and perform well (Elliott et al. 1995; this study) at sites where their abundance is consistently negligible. If they also occasionally spawn at high-elevation sites, which they presumably do, perhaps temperature conditions are unsuitable for a phase occurring between the egg and subadult stage. Because eggs incubate during extreme winter conditions and are the most temperature-sensitive life stage in the entire brown trout life cycle (Elliott 1994), we posit that the recruitment bottleneck occurs during the embryo stage. While brown trout survival through egg incubation decreases markedly below 4 °C (Ojanguren and Braña 2003), temperatures measured during the period of brown trout incubation (November–March) at upper Logan River reaches are well below this threshold (1–2 °C; Budy et al. 2003). Temperatures measured at sites dominated by brown trout are consistently between 3 and 4 °C. In conclusion, extreme cold incubation conditions may offer the best explanation for the lack of self-sustaining, local populations of brown trout at high elevations of our system as well as in other western North American streams (Vincent and Miller 1969; Rahel and Nibbelink 1999; de la Hoz Franco and Budy 2005).

The role of biotic interactions in zonation

We provide evidence for an asymmetric, negative effect of brown trout presence on cutthroat trout. Allopatric cutthroat trout attained higher condition and growth than did their sympatric counterparts at nearly all sites. Sympatric brown trout, in contrast, performed better than allopatric brown trout everywhere. Our use of a substitutive approach for assessing competition (Fausch 1998) indicates that interspecific competition (with brown trout) is more intense than intraspecific competition for cutthroat trout, while for brown trout the reverse is true. Further, the fact that the condition differential (between treatment groups) for brown trout was consistent (i.e., there was no reversal in competitive ability) at all temperatures suggests a lack of temperature-mediated

© 2005 NRC Canada

Table 5. Summary of experimental studies on temperature-mediated competition among salmonid species.

Upstream species	Downstream species	Arena (density)	Temperature range	Performance measure(s)	Main result(s)[a]	Reference
Greenback cutthroat trout (*Oncorhynchus clarkii pleuriticus*)	Brook trout (*Salvelinus fontinalis*)	1.8 m × 0.6 m lab stream (5.5 fish·m^{-2})	Constant 10 and 20 °C	Aggressive acts; microhabitat use; frequency of dominance	Brook > cutthroat (all responses) at 20 °C; at 10 °C, brook trout = cutthroat trout in microhabitat use and dominance frequency; there was temperature-mediation of aggression (i.e., brook trout were more aggressive at high temperatures; cutthroat trout were more aggressive at low temperatures)	De Staso and Rahel 1994
Brook trout	Rainbow trout (*Oncorhynchus mykiss*)	1-m^2 pools and riffles in a lab stream (2 fish·m^{-2})	Constant 13 and 18 °C	Aggressive acts; food acquisition; growth	Brook trout > rainbow trout for all response measures at both 13 and 18 °C	Magoulick and Wilzbach 1998*b*
Greenback cutthroat trout	Brook trout	190-L lab aquaria (12.7 fish·m^{-2})	Diel cycles of 1–8 °C and 9–17 °C	Food acquisition; aggressive acts; microhabitat use	Larger brook trout dominated overall, with greater aggression at 9–17 °C; greenback cutthroat trout never attained an advantage	Novinger 2000
Whitespotted char (*Salvelinus leucomaenis leucomaenis*)	Dolly Varden char (*Salvelinus malma*)	2.8 m × 0.35 m lab stream (51 fish·m^{-2})	Constant 6 and 12 °C	Aggressive acts; foraging frequency; microhabitat use; growth; survival	Whitespotted char generally dominated over Dolly Varden char across temperatures and responses; their effect was diminished at 6 °C, suggesting a mediating role of temperature	Taniguchi and Nakano 2000
Brook trout	Brown trout (*Salmo trutta*)	2 m × 0.6 m lab stream (2.5 fish·m^{-2})	Constant 3, 6, 10, 20, 22, 24, and 26 °C	Food acquisition; aggressive acts	Brook = brown at all temperatures; brook trout had greater mortality than brown trout because of high temperatures	Taniguchi et al. 1998
Bonneville cutthroat trout (*Oncorhynchus clarkii utah*)	Brown trout	20-m^2 in situ enclosures (0.40 fish·m^{-2})	Ambient cycle range: mean = 8–13 °C; min.–max. = 6.1–17.5 °C; see Table 2	Growth and condition	Brown trout were unaffected by cutthroat trout; cutthroat trout condition was reduced by brown trout at all temperatures, excluding 17.5 °C	This study

[a]"Species 1 > species 2" denotes that species 1 was a more successful competitor than species 2.

© 2005 NRC Canada

competitive resistance to brown trout invasions by cutthroat trout.

While the potential for cutthroat trout displacement from downstream habitats due to brook trout invasions is widely acknowledged (Dunham et al. 2002; Novinger and Rahel 2003; Quist and Hubert 2004), the potential for a similar effect of brown trout is rarely considered. Distributional patterns in the Bonneville Basin (de la Hoz Franco and Budy 2005) indicate that displacement may have occurred, and we provide insight into a possible mechanism. While we did not document the behavioral origin of brown trout impacts in our study, dominance via aggression (i.e., interference competition) is a likely candidate. In a lab study of brown trout – greenback cutthroat trout (*Oncorhynchus clarkii pleuriticus*) interactions, brown trout were more aggressive, attained the best foraging positions, and thereby suppressed cutthroat trout feeding (Wang and White 1994). In other studies, brown trout dominated over masu salmon (*Oncorhynchus masou masou*), whitespotted char (*Salvelinus leucomaenis leucomaenis*), and were unaffected by steelhead trout (*O. mykiss*; Kocik and Taylor 1994; Hasegawa et al. 2004). Brown trout are thus well established as a dominant competitor among salmonids.

In summary, we believe the downstream limit of cutthroat trout is determined by the presence of and their interactions with brown trout. Further, the observation that brown trout performed consistently better with cutthroat trout in our experiment indicates that temperature rather than competitive resistance likely explains the absence of brown trout from high elevations.

Salmonid temperature-mediated competition experiments

Temperature-mediated competition has been proposed as the primary cause of salmonid zonation in rivers and streams throughout the world (Fausch 1989; Fausch et al. 1994; de la Hoz Franco and Budy 2005). In addition to our field experiment, this proposition has been evaluated for several salmonids using a variety of performance responses (Table 5). Encompassing a wide range of temperatures and experimental densities, a simultaneous consideration of these studies illustrates two patterns. First, downstream species are superior competitors in two-species systems (but see Magoulick and Wilzbach 1998*b*); and second, reversals in dominance due to cold temperatures — whereby the upstream species attains superiority — rarely occur (but see De Staso and Rahel 1994).

The lack of a competitive reversal has been attributed to at least one of three causes. First, while competitive effects of downstream species may be dampened under cold conditions, temperatures may not have been sufficiently extreme to induce dominance reversals (Taniguchi et al. 1998; Taniguchi and Nakano 2000). The fact that reversals have not been observed at temperatures as low as 1–3 °C (see Table 5) indicates that this explanation is unlikely. Second, a common thermal physiology for both species might also prevent a competitive reversal (Novinger 2000). Given that thermal tolerance and temperature-related mortality differed among species in at least two studies (see Table 5) suggests that this, too, is an unlikely explanation.

Finally, the lack of a dominance reversal suggests that abiotic factors rather than temperature-mediated competition preclude downstream species from high-elevation reaches. Specifically, downstream species may be unable to avoid starvation (Taniguchi et al. 1998; Taniguchi and Nakano 2000) and (or) complete their entire life cycle (e.g., embryonic phases; De Staso and Rahel 1994; Novinger 2000) under cold conditions, even if juveniles or adults experience positive growth under short-term, experimental conditions. We believe that these are more plausible explanations for why reversals were rarely observed and are deserving of further scientific attention. In summary, our study adds to a growing body of evidence suggesting that salmonid zonation is not the result of condition-specific competition.

Implications for cutthroat trout conservation

The potential for negative effects of brown trout on cutthroat trout and the likely limitation of the present distribution of brown trout by abiotic conditions have important implications for the conservation of cutthroat trout. First, management actions involving the direct removal of brown trout should be considered if increasing the abundance and spatial extent of cutthroat trout is desirable (e.g., Lentsch et al. 1997). Such actions have been aggressively pursued for the conservation of cutthroat trout in the presence of invasive brook trout (Thompson and Rahel 1996; Novinger and Rahel 2003; Peterson et al. 2004), and the demographic benefits (e.g., increased age-0 cutthroat trout survival) are promising (Peterson et al. 2004). Thus, the eradication of exotic brown trout may benefit cutthroat trout where these species co-occur.

While brown trout invasions may have slowed in streams like the Logan River (i.e., they have had ~100 years to invade suitable habitats), this may change under future climatic and land-management scenarios. If temperatures increase, brown trout distributions may shift upstream (Keleher and Rahel 1996) and thus reduce the extent of remaining cutthroat trout populations. Indeed, brown trout distributions have been observed to change rapidly in invaded systems during periods of climate change (e.g., drought; Closs and Lake 1996). While there is little managers can do to affect climate, they can take measures to reduce water temperature changes related to land management (e.g., changes in vegetation, Theurer et al. 1984).

In conclusion, brown trout effects are currently recognized as only a minor threat to cutthroat trout persistence (Quist and Hubert 2004); secondarily to the respective hybridization and displacement impacts of rainbow and brook trout (Dunham et al. 2002; Weigel et al. 2003). However, we suggest that exotic brown trout invasions could have serious consequences for cutthroat trout. Thus, brown trout should be considered more explicitly in cutthroat trout conservation efforts.

Acknowledgments

We gratefully acknowledge Gary Thiede for logistical oversight. Rob Nunn, Sarah Carrothers, Ben Kuhns, Erin Vandyke, Ben Kennedy, and Robert Al-Chokhachy assisted with field work. We thank Susan Durham for her statistical insight during the design and analysis phases of our study.

© 2005 NRC Canada

Financial support was provided by the Utah Department of Natural Resources – Division of Wildlife Resources (Project XII, Sport Fisheries Research, Grant No. F-47-R, Segment 16), the US Geological Survey, the Quinney Foundation (fellowship to McHugh), and the Utah State University Community – University Research Initiative and Water Initiative programs. Todd Crowl, Mike Pfrender, Dan Rosenberg, Jack Schmidt, and Utah Cooperative Fish and Wildlife Research Unit (UT-CFWRU) members reviewed earlier drafts of this manuscript.

References

Behnke, R.J. 1992. Native trout of western North America. Am. Fish. Soc. Monogr. 6.

Benke, A.C., Huryn, A.D., Smock, L.A., and J.B. Wallace. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. J. N. Am. Benthol. Soc. **18**: 308–343.

Bozek, M.A., and Hubert, W.A. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. Can. J. Zool. **70**: 886–890.

Budy, P.B., de la Hoz Franco, E., Thiede, G.P., and Vatland, S. 2003. Logan River whirling disease study: factors affecting trout population dynamics, abundance, and distribution in the Logan River, Utah. Annual Report to Utah Division of Wildlife Resources. Utah Cooperative Fish and Wildlife Research Unit, Logan, Utah.

Budy, P.B., McHugh, P., and Thiede, G.P. 2004. Logan River whirling disease study: factors affecting trout population dynamics, abundance, and distribution in the Logan River, Utah. Annual Report to Utah Division of Wildlife Resources. Utah Cooperative Fish and Wildlife Research Unit, Logan, Utah.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag Inc., New York.

Closs, G.P., and Lake, P.S. 1996. Drought, differential mortality and the coexistence of a native and an introduced fish species in a south east Australian intermittent stream. Environ. Biol. Fishes, **47**: 17–26.

de la Hoz Franco, E.A., and Budy, P. 2005. Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient. Environ. Biol. Fishes, **72**: 379–391.

De Staso, J., III, and Rahel, F.J. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. Trans. Am. Fish. Soc. **123**: 289–297.

Duff, D.A. 1988. Bonneville cutthroat trout: current status and management. Am. Fish. Soc. Symp. **4**: 121–127.

Dunham, J., Adams, S.B., Schroeter, R., and Novinger, D. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and their potential impacts on inland cutthroat trout in western North America. Rev. Fish. Biol. Fish. **12**: 373–391

Dunson, W.A., and Travis, J. 1991. The role of abiotic factors in community organization. Am. Nat. **138**: 1067–1091.

Elliott, J.M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford, UK.

Elliott, J.M., and Hurley, M.A. 2000. Daily energy intake and growth of piscivorous brown trout, *Salmo trutta*. Freshw. Biol. **44**: 237–245.

Elliott, J.M., Hurley, M.A., and Fryer, R.J. 1995. A new, improved growth model for brown trout, *Salmo trutta*. Funct. Ecol. **9**: 290–298.

Fausch, K.D. 1989. Do gradient and temperature affect distribution of, and interactions between juvenile brook char and other salmonids in streams? Physiol. Ecol. Jpn. Spec. **1**: 303–322.

Fausch, K.D. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating evidence across scales. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 218–231.

Fausch, K.D., Nakano, S., and Ishigaki, K. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. Oecologia, **100**: 1–12.

Gresswell, R.E. 1988. Status and management of interior stocks of cutthroat trout. Ame. Fish. Soc. Symp. No. 4.

Hasegawa, K., Yamamoto, T., Murakami, M., and Maekawa, K. 2004. Comparison of competitive ability between native and introduced salmonids: evidence from pairwise contests. Ichthyol. Res. **51**: 191–194.

Jobling, M. 1981. Temperature and the final preferendum — rapid methods for the assessment of optimum growth temperatures. J. Fish. Biol. **19**: 439–455.

Johnstone, H.C., and Rahel, F.J. 2003. Assessing temperature tolerance of Bonneville cutthroat trout based on constant and cycling thermal regimes. Trans. Am. Fish. Soc. **132**: 92–99.

Keleher, C.J., and Rahel, F.J. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a Geographic Information System (GIS) approach. Trans. Am. Fish. Soc. **125**: 1–13.

Kocik, J.F., and Taylor, W.W. 1994. Summer survival and growth of brown trout with and without steelhead under equal total salmonine densities in an artificial stream. Trans. Am. Fish. Soc. **123**: 931–938.

Lentsch, L., Converse, Y., and Perkins, J. 1997. Conservation agreement and strategy for Bonneville cutthroat trout (*Oncorhynchus clarki utah*) in the state of Utah. Utah Division of Wildlife Resources, Salt Lake City, Utah. Publ. No. 97–19.

Magoulick, D.D., and Wilzbach, M.A. 1998*a*. Are native brook charr and introduced rainbow trout differentially adapted to upstream and downstream reaches? Ecol. Freshw. Fish. **7**: 167–175.

Magoulick, D.D., and Wilzbach, M.A. 1998*b*. Effect of temperature and microhabitat on interspecific aggression, foraging success, and growth of brook trout and rainbow trout pairs in laboratory streams. Trans. Am. Fish. Soc. **127**: 708–717.

Novinger, D.C. 2000. Reversals in competitive ability: Do cutthroat trout have a thermal refuge from competition with brook trout? Ph.D. dissertation, University of Wyoming, Laramie, Wyoming.

Novinger, D.C., and Rahel, F.J. 2003. Isolation management with artificial barriers as a conservation strategy for cutthroat trout in headwater streams. Conserv. Biol. **17**: 772–781.

Ojanguren, A.F., and Braña, F. 2003. Thermal dependence of embryonic growth and development in brown trout. J. Fish. Biol. **62**: 580–590.

Ojanguren, A.F., Reyes-Gavilan, F.G., and Brana, F. 2001. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. J. Therm. Biol. **26**: 165–170.

Peterson, D.P., Fausch, K.D., and White, G.C. 2004. Population ecology of an invasion: effects of brook trout on native cutthroat trout. Ecol. Appl. **14**: 754–772.

Quist, M.C., and Hubert, W.A. 2004. Bioinvasive species and the preservation of cutthroat trout in the western United States: ecological, social, and economic issues. Environ. Sci. Pol. **7**: 313–313.

Rahel, F.J., and Hubert, W.A. 1991. Fish assemblages and habitat gradients in a Rocky Mountain – Great Plains stream: biotic

© 2005 NRC Canada

zonation and additive patterns of community change. Trans. Am. Fish. Soc. **120**: 319–332.

Rahel, F.J., and Nibbelink, N.P. 1999. Spatial patterns in relations among brown trout (*Salmo trutta*) distribution, summer air temperature, and stream size in Rocky Mountain streams. Can. J. Fish. Aquat. Sci. **56**(Suppl. 1): 43–51.

SAS Institute Inc. 2002. SAS version 8.02. SAS Institute Inc., Cary, N.C.

Schrank, A.J., Rahel, F.J., and Johnstone, H.C. 2003. Evaluating laboratory-derived thermal criteria in the field: an example involving Bonneville cutthroat trout. Trans. Am. Fish. Soc. **132**: 100–109.

Taniguchi, Y, and Nakano, S. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. Ecology, **81**: 2027–2039.

Taniguchi, Y., Rahel, F.J., Novinger, D.C., and Gerow, K.G. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Can. J. Fish. Aquat. Sci. **55**: 1894–1901.

Theurer, F.D., Voos, K.A., and Miller, W.J. 1984. Instream water temperature model. US Fish and Wildlife Service, Fort Collins, Colorado. Instream Flow Inf. Pap. 16, FWS/OBS-84/15.

Thompson, P.D., and Rahel, F.J. 1996. Evaluation of depletion–removal electrofishing of brook trout in small Rocky Mountain streams. N. Am. J. Fish. Manag. **16**: 332–339.

Vannote, R.L., Marshall, G., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. Can. J. Fish Aquat. Sci. **37**: 130–137.

Vincent, R.E., and Miller, W.H. 1969. Altitudinal distribution of brown trout and other fishes in a headwater tributary of the South Platte River, Colorado. Ecology, **50**: 464–466.

Wagner, E.J., Arndt, R., Routledge, M.D., and Bradwisch, Q. 1998. Hatchery performance and fin erosion of Bonneville cutthroat trout, *Oncorhynchus clarki*, at two temperatures. J. Appl. Aqua. **8**: 1–12.

Wagner, E.J., Arndt, R.E., and Brough, M. 2001. Comparative tolerance of four stocks of cutthroat trout to extremes in temperature, salinity, and hypoxia. West. N. Am. Nat. **61**: 434–444.

Wang, L., and White, R.J. 1994. Competition between wild brown trout and hatchery greenback cutthroat trout of largely wild parentage. N. Am. J. Fish. Manag. **14**: 475–487.

Weigel, D.E., Peterson, J.T., and Spruell, P. 2003. Introgressive hybridization between native cutthroat trout and introduced rainbow trout. Ecol. Appl. **13**: 38–50.

Wolman, M.G. 1954. A method of sampling coarse river-bed material. Trans. Am. Geo. Un. **35**: 951–956.

Young, M.K. 1995. Conservation assessment for inland cutthroat trout. US Dep. Agric. For. Serv. Rocky Mt. For. Range Exp. St. RM-GTR-256.

© 2005 NRC Canada

Parasitism, space constraints, and gonad asymmetry in the pollan (*Coregonus autumnalis*)

Chris Harrod and David Griffiths

Abstract: Both sexes of Lough Neagh pollan (*Coregonus autumnalis*) show directional asymmetry in gonad mass, the left being larger than the right in 70% of individuals. The frequency and degree of asymmetry are size independent in males but become progressively more marked in females of >120 g somatic mass. There is little evidence to support the hypothesis that the size of the body cavity constrains gonad size. Pollan are heavily and size-dependently infected by metacercariae of the trematode *Ichthyocotylurus erraticus*. Total gonad mass in both sexes of pollan is negatively correlated with infection intensity of this parasite. In females, mean egg size shows no trend but fecundity declines and the degree of asymmetry in ovary mass increases with infection intensity up to a threshold, beyond which it remains constant. While directional asymmetry in gonad size is strongly developmentally controlled in many fish species, variation in the degree of gonad asymmetry in pollan provides a potentially sensitive indicator of stress.

Résumé : Les deux sexes du pollan (*Coregonus autumnalis*) au Lough Neagh présentent une asymétrie directionnelle de la masse de leurs gonades, la gauche étant plus grande que la droite chez 70 % des individus. La fréquence et l'importance de l'asymétrie sont indépendantes de la taille chez les mâles, mais elles deviennent progressivement plus marquées chez les femelles de masse somatique >120 g. Il y a peu d'indications pour appuyer l'hypothèse selon laquelle la dimension de la cavité corporelle restreint la taille des gonades. Les pollans sont fortement infectés par les métacercaires du trématode *Ichthyocotylurus erraticus* et l'infection varie en fonction de la taille. Il y a une corrélation négative entre la masse totale des gonades chez les pollans et l'intensité de l'infection par ce parasite. Chez les femelles, la taille moyenne des oeufs ne suit aucune tendance particulière; en revanche, la fécondité décline et l'importance de l'asymétrie de la masse ovarienne augmente en fonction de la gravité de l'infection jusqu'à une limite supérieure au-delà de laquelle elles demeurent constantes. Bien que l'asymétrie directionnelle de la taille des gonades soit fortement contrôlée par le développement chez plusieurs espèces de poissons, la variation de l'importance de l'asymétrie des gonades chez les pollans fournit un indicateur potentiellement sensible du stress.

[Traduit par la Rédaction]

Introduction

Asymmetries in paired structures are subject to both genetic and environmental influences. In some species, the asymmetry is largely under developmental or genetic control and extreme. For example, there is no left testis in most *Oryzias* species (Hamaguchi 1996), the left ovary has more or less disappeared in mbuna, the rock-frequenting group of cichlid species in Lake Malawi (Fryer and Iles 1972), and only the right ovary is functional in six genera of cartilaginous fishes and only the left in two genera (Dodd 1983). Other asymmetries are less extreme and have attracted much attention recently because they have been shown to be influenced by environmental factors (Clarke 1995; Møller 1997). Fluctuating asymmetry has most frequently been examined as a measure of environmental stress, but variation in the degree of directional asymmetry has also been linked to stress (Sasal and Pampoulie 2000). However, directional asymmetry in internal structures such as gonads, in a body cavity of finite size, could also be a consequence of space constraints (Brown and Kamp 1942; MacGregor 1968). The distended abdomens characteristic of gravid female fish close to spawning time suggest that abdominal space might limit ovary size and affect symmetry.

Directional gonad asymmetry has been observed in whitefish (*Coregonus lavaretus*) (Heese 1990), salmonids (*Oncorhynchus* spp.) (Rounsefell 1957; A. Hendry, Department of Biology, McGill University, Montréal, QC H3A 2K6, Canada, unpublished data), Atlantic salmon (*Salmo salar*) (C. Harrod, personal observation), brown trout (*Salmo trutta*) (Brown and Kamp 1942), and other fishes, e.g., anguillid eels (Tesch 2003), anchovies (*Anchoa naso*, *Engraulis mordax*, and *Engraulis encrasicolus*) (MacGregor 1968; Vallisneri and Scapolatempo 2000), capelin (*Mallotus villosus*) (Winters 1971), and albacore (*Thunnus alalunga*) (Ramon and Bailey 1996). In most species, the left gonad is larger than the right.

Asymmetry in paired fins has been correlated with reproductive effects (Hechter et al. 2000; Wedekind and Müller 2004) and with parasitism (Reimchen 1997; Sasal and Pampoulie 2000). Parasitism can affect fish physiology and

Received 6 October 2004. Accepted 19 May 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 2 November 2005.
J18341

C. Harrod[1] and D. Griffiths.[2] School of Environmental Sciences, University of Ulster, Coleraine, BT52 1SA, UK.

[1]Present address: Department of Physiological Ecology, Max Planck Institute for Limnology, Postfach 165, 24302 Plön, Germany.
[2]Corresponding author (e-mail: d.griffiths@ulster.ac.uk).

 doi: 10.1139/F05-175 © 2005 NRC Canada

reproductive potential (e.g., Arme and Owen 1968; Pampoulie et al. 1999; Tolonen et al. 2002), but parasitism has not been associated with gonad asymmetry.

Pollan (Arctic cisco in North America) (*Coregonus autumnalis*) occur as glacial relicts in Ireland, far outside their main high arctic range, and are subject to a variety of environmental stressors, both external and internal (Harrod et al. 2001, 2002; Harrod and Griffiths 2005). Almost all adult fish in Lough Neagh (99.9% of fish older than 1+, n = 2126) are infected with metacercariae of a trematode, *Ichthyocotylurus erraticus*, at densities (median infection intensity, i.e., the number of parasites per fish, 536 in fish 2+ and older) considerably greater than those shown to cause death or reduced condition in other fish species (Harrod and Griffiths 2005). The pericardial aggregations of the parasite probably affect heart function, and this, coupled with low oxygen concentrations in hypertrophic Lough Neagh, could reduce fitness by affecting survival, condition, or reproduction. Females are more heavily infected than males. *Ichthyocotylurus erraticus* affects somatic condition and liver size in pollan (Harrod and Griffiths 2005) and condition, liver, and reproductive indices and heart mass in *C. lavaretus* in Loch Lomond (Dolezel and Crompton 2000).

Harrod and Griffiths (2004) described the reproductive biology of pollan in Lough Neagh, the only stock to have been examined in detail. This paper describes patterns of gonad asymmetry in pollan and investigates to what extent space constraints and parasitism are correlated with these patterns. We find no support for the space constraints hypothesis but demonstrate differences in the pattern of asymmetry between male and female fish and show that asymmetry in females is linked to infection intensity.

Materials and methods

Pollan were sampled from Lough Neagh (6°25′W, 54°35′N) using surface- and bottom-set multipanel gill nets on five occasions from September to early December 1999, when fish normally spawn. Fish were aged from scales following the procedure of Wilson and Pitcher (1984). The contents of the body cavity were divided into gonads, liver, and alimentary canal and each weighed separately to the nearest 0.01 g. Sex was assessed through visual inspection of the gonads. Left and right gonads of 136 female and 94 male fish were weighed individually. Ripe ovaries (maturation stage 5; Lagler 1978) were stored individually in Bouin's fixative prior to measurement of egg size and fecundity. Pollan hearts and any encysted *Ichthyocotylurus* metacercariae found in the pericardial cavity were stored in 80% alcohol. To measure infection intensity, cysts were teased from the heart and host reactive tissue using mounted needles and this material squeezed between microscope slides before counting cysts under a low-power microscope.

Asymmetry was measured as the signed difference between left and right gonad mass, the signed difference expressed as a percentage of the left gonad mass or the ratio of left to right gonad mass. Most analyses were restricted to fish with ripe gonads (stage 5). When investigating the effect of parasitism, the analysis was restricted to fish collected shortly before spawning (November) for which all three measures of reproductive potential (i.e., ovary size, egg size, and fecundity) were available.

Asymmetry might vary with fish size (Somarakis et al. 1997). Two measures of fish size were used to detect effects on gonads and on the body cavity contents. When examining relationships between body cavity components, gutted mass (i.e., total body mass minus body cavity content mass) was used as the independent variable, while in investigations of possible parasite effects on gonads, somatic mass (i.e., total body mass minus gonad mass) was used. Regressions of right versus left gonad mass were carried out: this tests for a fish size effect, since gonad size is correlated with fish size (see below). Slopes of log-transformed gonad mass regressions significantly different from 1 indicate that there is a body size effect, while intercepts significantly different from 1 indicate asymmetry. To show nonlinear trends, locally weighted scatterplot smoothing (LOWESS) was used. To test the possibility, suggested by the data, that the degree of asymmetry (Y) changes above a threshold body size or infection intensity (X), linear and piecewise (Toms and Lesperance 2003) models

$$Y = a + bX$$

$$Y = a + b_1X + b_2(X - T) \qquad (X > T)$$

were fitted to the data using nonlinear least squares regression. The terms in parentheses in the piecewise model control where the change in slope (T) occurs. The small-sample Akaike's Information Criterion (AIC_c) was calculated for each model because the ratio of number of observations to number of estimated parameters was appreciably below 40 for most data sets. Model fits were then compared with AIC_c, Akaike weights, and evidence (Akaike weight) ratios (Burnham and Anderson 1998). Since gonad size, infection intensity, and degree of asymmetry varied with body size and age, the effects of the latter were controlled for by partial correlation. All errors are standard errors.

Results

Paired t tests showed left gonad masses to be significantly larger than right in both sexes (Table 1): the percent difference was much greater in females. Note, however, that the right gonads were larger than the left in about one third of the fish (Fig. 1). In the absence of estimates of measurement error, we assumed that gonads were asymmetric if they differed in mass by more than 10%: about 70% of fish showed differences of this magnitude or greater. The distribution of differences between left and right gonad masses in female or male fish in gonad state 5 showed no significant skewness or kurtosis.

The pattern of asymmetry differs between the sexes (Table 2): the degree of gonad asymmetry was size dependent in females but not in males. Note that this conclusion does not depend on whether ordinary least squares or reduced major axis regression is used. The frequency of ovarian asymmetry was also size dependent. Only half of the 20 smallest fish examined (maximum somatic mass 129 g) had larger left ovaries, but this had risen to 85% for the 20 largest fish (minimum somatic mass 177 g) and one fish had symmetrical ovaries.

© 2005 NRC Canada

Table 1. Comparison of left and right gonads of pollan (*Coregonus autumnalis*) in maturity stage 5.

Sex	Mean left gonad mass (g)	Mean right gonad mass (g)	% difference	*n*	*t*	*P*	% fish with left > right
Female	12.85	11.43	11.1	76	4.10	<0.001	68
Male	1.08	1.01	6.5	60	2.51	0.02	68

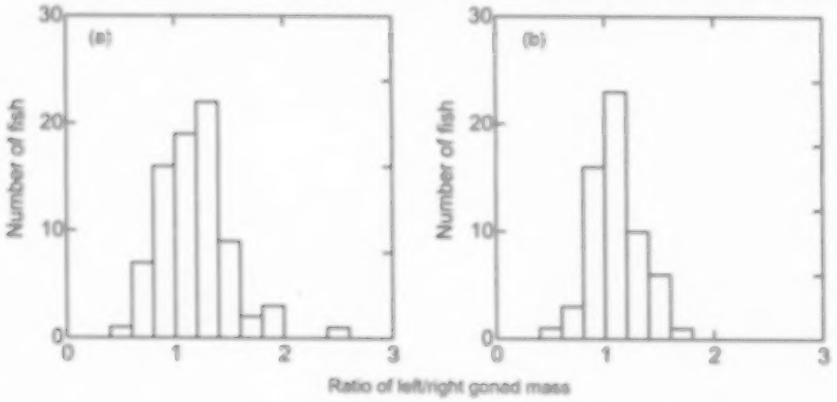
Note: The paired *t* tests were performed on log-transformed data but the reported masses are the back-transformed values.

Table 2. Summary of regression statistics of log right pollan gonad mass against log left gonad mass.

Sex	$a \pm$ SE	t ($a = 0$)	*P*	OLS $b \pm$ SE	t ($b = 1$)	*P*	RMA *b*	*n*
Female	0.184±0.057	3.23	<0.01	0.788±0.051	4.10	<0.001	0.901	76
Male	–0.025±0.012	2.12	<0.05	0.871±0.079	1.64	>0.10	1.058	60

Note: OLS, ordinary least squares; RMA, reduced major axis.

Fig. 1. Histograms of left to right gonad mass ratios for (*a*) male and (*b*) female pollan (*Coregonus autumnalis*).



Size-linked asymmetry was much more marked in ripe fish but was still significant in fish with late-developing ovaries (Fig. 2). However, the degree of asymmetry, when expressed as a percentage of left gonad mass, did not differ between fish of a given somatic mass in the two gonad states (analysis of covariance: slopes, $F_{[1,190]} = 0.44$; intercepts, $F_{[1,191]} = 2.52$). For fish with ripe ovaries, piecewise regression gave a better fit than the linear model ($AIC_c = 3.90$). The Akaike weights (0.87 and 0.12) show that the piecewise model is seven times more likely to be the better model. Ovarian asymmetry did not appear until fish reached a somatic mass of 120 ± 12 g, equivalent to a fork length of 235 mm (age 2+ fish).

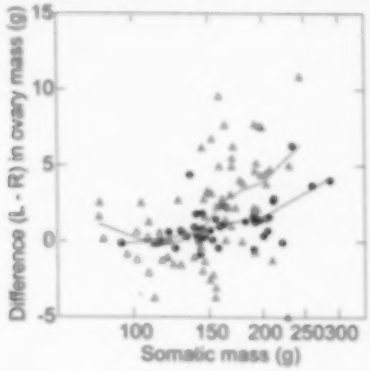
The ratio of left to right gonad size varied with somatic mass, but the slope and intercept of this relationship did not depend on sampling date (slopes, $F_{[4,100]} = 1.23$; intercepts, $F_{[4,104]} = 0.43$). Hence, the degree of asymmetry in gonad size did not vary over the sampling period (1 September to 21 November 1999) despite total gonad mass, adjusted for fish size, increasing by a factor of 3.5 over this period.

Body cavity components varied strongly with body size, as did the number of *Ichthyocotylurus* (Table 3). Ovary, gut, and liver increased in size with gutted mass at the same rate (analysis of covariance: slopes, $F_{[2,92]} = 1.20$, $P > 0.05$). Ovary and combined gut and liver masses were positively correlated ($r = 0.60$, $P < 0.01$, $n = 22$), but this relationship disappeared after controlling for gutted mass (partial $r = -0.23$). Similarly, there were no significant partial correlations between right or left ovary masses or the size difference in ovary mass and combined gut and liver mass when gutted mass was controlled (i.e., there was no evidence of a body cavity size constraint).

Ichthyocotylurus numbers increased with gonad size in both sexes: the slopes and intercepts did not differ between the sexes. Partial correlations were calculated to control for the effect of somatic mass. Gonad mass declined with increasing *Ichthyocotylurus* numbers in both sexes (male partial $r = -0.38$, 26 df, $P < 0.05$; female partial $r = -0.72$, 17 df, $P < 0.001$) (Fig. 3). *Ichthyocotylurus* numbers were not correlated with gonad asymmetry in males, but females were affected: the difference between right and left gonad masses expressed in absolute (or percentage) terms increased with the number of *Ichthyocotylurus* to a plateau (Fig. 4). Piecewise regression gave a better fit to these data than the linear model ($AIC_c = 4.76$): the Akaike weights (0.92 and 0.08) show that the piecewise model is 11 times more likely to be the better model. The degree of asymmetry in gonad size was significantly correlated with the number of parasites below the breakpoint of 855 (±213) parasites per fish ($r = 0.58$, $P < 0.01$, $n = 25$) and the intercept was not significantly different from 0 ($a = 0.90 \pm 0.88$) (i.e., uninfected fish had symmetrical ovaries). Increasing ovarian asymmetry with infection intensity in fish with less than 855 *Ichthyocotylurus* was not related to fish size or age. There was no

© 2005 NRC Canada

Fig. 2. The degree of gonad size asymmetry varies with fish size in female pollan (*Coregonus autumnalis*) with late-maturing ovaries (circles) and ripe ovaries (triangles).



change in the degree of asymmetry for fish with larger infection intensities (mean difference in ovary mass = 18.7% ± 3.8%).

Mean egg size (diameter) did not differ between left and right ovaries (paired t test: $t = 0.52$, 61 df). Egg size increased with fish mass and infection intensity ($r = 0.58$, 35 df, $P < 0.001$, and $r = 0.43$, 35 df, $P < 0.01$, respectively), but after controlling for mass, there was no parasite effect (partial $r = 0.17$). Egg size was independent of fish size for any age of fish (i.e., egg size was not related to growth rate). There was no correlation between skewness in egg size of left and right ovaries ($r = 0.16$, $P > 0.05$, $n = 116$). Skewness increased as ovaries developed ($r = 0.48$, $P < 0.001$, $n = 116$): skewness was correlated with gonad mass when somatic mass was controlled for (partial $r = 0.52$, 88 df, $P < 0.001$). However, skewness was not related to infection intensity after controlling for somatic mass (partial $r = -0.06$, 66 df).

Fecundity declined slowly and egg size increased rapidly as spawning date approached (log fecundity = 2.50 – 0.0011 ± 0.0004 × day + 0.79 ± 0.10 × log somatic mass ($R^2 = 0.43$, $n = 84$), log egg diameter = –1.18 – 0.0030 ± 0.0002 × day + 0.24 ± 0.05 × log somatic mass ($R^2 = 0.77$, $n = 84$), where day is the number of days since 1 January 1999). There was a significant negative correlation between egg size and fecundity after controlling for body size and day (partial $r = -0.38$, 80 df, $P < 0.001$). Fecundity declined with increasing infection intensity (Fig. 5) when the effect of somatic mass was controlled (partial $r = -0.59$, 34 df, $P < 0.001$).

Discussion

The literature contains a number of vague references to the effect that gonad asymmetry is not uncommon in fishes (e.g., MacGregor 1968; Sanwal and Khanna 1972; Ramon and Bailey 1996), but there is insufficient information to determine its frequency. In species in which both gonads develop, the ovary size ratio ranges from 8.8 in capelin (Winters 1971) to around 1.3 in trout, anchovies, and pollan (Brown and Kamp 1942; MacGregor 1968; Vallisneri and Scapolatempo 2000). The left gonad is usually the larger (11/14 species), suggesting some general constraint (whether physical or phylogenetic; Harvey and Pagel 1993). However,

Table 3. Regression slopes of pollan body cavity components as a function of gutted mass and infection intensity as a function of somatic mass (all variables log transformed; all fish in gonad state 5 collected on 10–11 November 1999).

	b	r^2	n	P
Ovary mass	1.375±0.229	0.64	22	<0.001
Testis mass	0.969±0.178	0.73	13	<0.001
Gut mass	1.400±0.186	0.62	37	<0.001
Liver mass	1.915±0.180	0.76	37	<0.001
Infection intensity	2.592±0.429	0.52	36	<0.001

geographic variation in the degree (capelin, Winters 1971; albacore, Ramon and Bailey 1996) and even direction (sockeye salmon (*Oncorhynchus nerka*), Rounsefell 1957) of asymmetry has been reported, consistent with an environmental influence.

Pollan provide only very limited support for the space constraint hypothesis. The testes were more symmetrical than the much larger ovaries as predicted by this hypothesis, but the ovaries did not become more asymmetrical as they developed and spawning date approached (although absolute size differences did increase). In November, the ovaries constituted a median of 69.5% ($n = 50$) of the mass of the body cavity contents. MacGregor (1968) argued that since gonads are the last organs to develop in the body cavity, they will occupy whatever space is available. Brown and Kamp (1942) noted that gonad asymmetry in female *S. trutta* was associated with the anatomical configuration of the intestine, which, in its posterior region, bends to one side (usually the right). Pollan might be similarly affected, but we have no information on the orientation of the anterior portion of the intestine. While the left gonad was larger in most pollan, consistent with this explanation, the converse was true in about 30% of fish. There is probably little selective pressure on internal (gonad) asymmetry but strong pressure on external morphology, since this is likely to affect swimming ability. If this is correct, internal asymmetry in one organ would be expected to necessitate a compensatory asymmetry in other internal structures. However, there was no evidence of such compensation in pollan. If the other body cavity structures differ in their compressibility, one might expect the degree of asymmetry to change as ovaries develop, but we found no support for a temporal change in relative asymmetry. Furthermore, if, as our results suggest, egg number is largely determined early in the reproductive cycle and well before egg size (Kinnison et al. 2001), space constraints are unlikely to be important. The negative correlation between fecundity and egg size after controlling for body size is consistent with a space constraint. However, this seems unlikely to be the cause, since the correlation occurred both early (September) and late (November) in the reproductive cycle despite a threefold increase in gonad mass over this period: the correlation seems more likely to reflect an energetic trade-off.

This study shows that variation in the degree of directional asymmetry is associated with parasite infection intensity in females but not in males. While asymmetry was independent of fish size and not affected by infection intensity in male pollan, total testis mass declined with increasing levels of parasitism. Total ovary mass was also correlated

© 2005 NRC Canada

Fig. 3. (*a*) Pollan (*Coregonus autumnalis*) testis and (*b*) ovary masses decline with increasing numbers of *Ichthyocotylurus* after controlling for the effects of body size (log somatic mass).

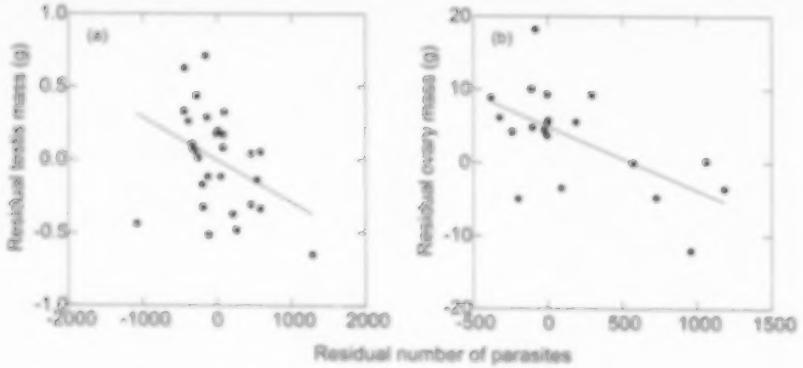


Fig. 4. Change in absolute asymmetry in pollan (*Coregonus autumnalis*) ovary mass as a function of infection intensity.

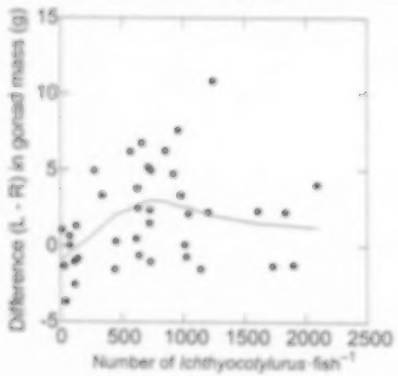
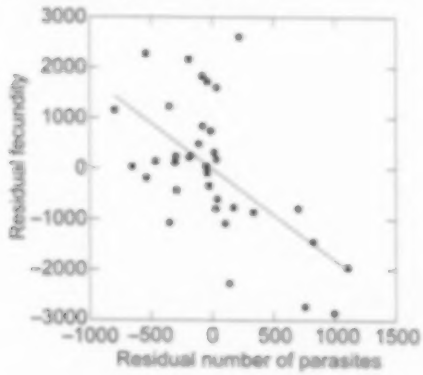


Fig. 5. Pollan (*Coregonus autumnalis*) fecundity declines with increasing numbers of *Ichthyocotylurus* after controlling for the effects of body size (log somatic mass).



with parasitism, and asymmetry increased above a fish size threshold because infection intensity was itself fish size dependent. Fecundity declined strongly with increasing parasite numbers, but there was no asymmetry in egg size or evidence that infection intensity affected egg size. The extremely high infection intensities observed (median intensity 536 and range 5–3941 in fish 2 or more years old and with 10% of fish more than twice the median) suggest that *Ichthyocotylurus* has a minor effect on survival, although there are clear energetic effects, with both somatic and liver condition being reduced (Harrod and Griffiths 2005). However, the mechanism by which parasitism generates the gonad asymmetry is unknown. While it is tempting to conclude that parasitism by *Ichthyocotylurus* reduces fitness by affecting gonad size, we have insufficient information to estimate lifetime reproductive success and the correlations do not exclude the possibility that fish that are stressed for other reasons are also more susceptible to parasitism.

Pollan were also attacked, less frequently, by the small intestinal cestode *Proteocephalus exiguus* (45% of fish) and the ectoparasitic copepod *Argulus foliaceus* (0.3%). Infection intensity by *Proteocephalus* was far less than by *Ichthyocotylurus*, with no sign of gut distortion, and consequently, we have assumed that the latter had the major impacts. Lough Neagh supports large numbers of waterbirds, which are the final host of *Ichthyocotylurus*, and one would expect greater gonad symmetry in populations with lower infection intensities. Unfortunately, there is no information on relative gonad sizes in the other three, endangered, Irish populations or on the species in its normal, high arctic range.

One might expect reproductive traits to be more sensitive indicators of biotic stress than meristic traits. The latter are subject to effects throughout the life of the fish and these traits might well be determined in the early stages of development. However, gonad development only occurs in larger individuals and is probably determined on an annual, rather than a whole life, basis. The asymmetry in pollan gonads is consistent with this possibility: the majority of small fish showed relatively low levels of infection by *Ichthyocotylurus* (Harrod and Griffiths 2005) and symmetric gonads, but the intensity of infection increased dramatically for fish larger than 200 mm fork length. However, as the earlier discussion makes clear, gonad asymmetry is not always an indicator of stress.

We have demonstrated that variation in the degree of gonad asymmetry and in fecundity is associated with levels of biotic stress (parasite infection intensity) in one species. We suggest that such measures have the potential to act as sensitive indicators of stress. The study highlights the need for more systematic reporting of inter- and intra-specific varia-

© 2005 NRC Canada

tion in relative gonad sizes and examination of the factors that influence that asymmetry.

Acknowledgements

Many thanks go to Andrew Hendry, Colin Adams, Chris Goldspink, Sam Irwin, and two anonymous referees for helpful comments on the manuscript and to the staff and students of the former Limnology Laboratory for practical help. Lough Neagh Fishermen's Co-operative and the Department of Agriculture, Northern Ireland (DANI) gave permission to fish. C.H. was funded through a Department of Education, Northern Ireland (DENI) postgraduate research studentship.

References

Arme, C., and Owen, R.W. 1968. Occurrence and pathology of *Ligula intestinalis* infections in British fishes. J. Parasitol. **54**: 272–280.

Brown, C.J.D., and Kamp, G.C. 1942. Gonad measurements and egg counts of brown trout (*Salmo trutta*) from the Madison River, Montana. Trans. Am. Fish. Soc. **71**: 195–200.

Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Clarke, G.M. 1995. Relationships between developmental stability and fitness: application for conservation biology. Conserv. Biol. **9**: 18–24.

Dodd, J. M. 1983 Reproduction in cartilaginous fishes (Chondrichthyes). *In* Fish physiology. Vol. 9A. *Edited by* W.S. Hoar, D.J. Randall, and E.M. Donaldson. Academic Press, New York. pp. 31–95.

Dolezel, M.C., and Crompton, D.W.T. 2000. Platyhelminth infections in powan, *Coregonus lavaretus* (L.), from Loch Eck and Loch Lomond, Scotland. Helminthologia, **37**: 147–152.

Fryer, G., and Iles, T.D. 1972. The cichlid fishes of the Great Lakes of Africa. Oliver and Boyd, Edinburgh.

Hamaguchi, S. 1996. Bilaterally asymmetrical testes in fishes of the genus *Oryzias*. Zool. Sci. (Tokyo), **13**: 757–763.

Harrod, C., and Griffiths, D. 2004. Reproduction and fecundity of the Irish pollan (*Coregonus autumnalis* Pallas, 1776), a threatened lake coregonid. Ann. Zool. Fenn. **41**: 117–124.

Harrod, C., and Griffiths, D. 2005. *Ichthyocotylurus erraticus* (Digenea: Strigeidae): factors affecting infection intensity and the effects of infection on pollan (*Coregonus autumnalis*), a glacial relict fish. Parasitology, **131**: 511–519.

Harrod, C., Griffiths, D., McCarthy, T.K., and Rosell, R. 2001. The Irish pollan, *Coregonus autumnalis*: options for its conservation. J. Fish Biol. **59**(Suppl. A): 339–355.

Harrod, C., Griffiths, D., Rosell, R., and McCarthy, T.K. 2002. Current status of the pollan (*Coregonus autumnalis* Pallas 1776) in Ireland. Arch. Hydrobiol. Spec. Issue Adv. Limnol. **57**: 627–638.

Harvey, P.H., and Pagel, M.D. 1993. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Hechter, R.P., Moodie, P.F., and Moodie, G.E.E. 2000. Pectoral fin asymmetry, dimorphism and fecundity in the brook stickleback, *Culaea inconstans*. Behaviour, **137**: 999–1009.

Heese, T. 1990. Gonad development and fecundity of whitefish *Coregonus lavaretus* (L. 1758) from the Pomeranian Bay. Acta Ichthyol. Pisc. **20**: 3–12.

Kinnison, M.T., Unwin, M.J., Hendry, A.P., and Quinn, T.P. 2001. Migratory costs and the evolution of egg size and number allocation in new and indigenous salmon populations. Evolution, **55**: 1656–1667.

Lagler, K.F. 1978. Capture, sampling and examination of fishes. *In* Methods for assessment of fish production in fresh waters. *Edited by* T. Bagenal. Blackwell Scientific Publications, Oxford. pp. 7–47.

MacGregor, J.S. 1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. Calif. Fish Game, **54**: 281–288.

Møller, A.P. 1997. Developmental stability and fitness. Am. Nat. **149**: 916–932.

Pampoulie, C., Morand, S., Lambert, A., Rosecchi, E., Bouchereau, J.L., and Crivelli, A.J. 1999. Influence of the trematode *Aphalloides coelomicola* Dollfus, Chabaud and Golvan, 1957 on the fecundity and survival of *Pomatoschistus microps* (Krøyer, 1838) (Teleostei: Gobiidae). Parasitology, **119**: 61–67.

Ramon, D., and Bailey, K. 1996. Spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific Ocean. Fish. Bull. **94**: 724–733.

Reimchen, T.E. 1997. Parasitism of asymmetrical pelvic phenotypes in stickleback. Can. J. Zool. **75**: 2084–2094.

Rounsefell, G.A. 1957. Fecundity of North American Salmonidae. Fish. Bull. U.S. Fish Wildl. Serv. **122**: 451–468.

Sanwal, R., and Khanna, S.S. 1972. Seasonal changes in the testes of a freshwater fish *Channa gachua*. Acta Anat. **83**: 139–148.

Sasal, P., and Pampoulie, C. 2000. Asymmetry, reproductive success and parasitism of *Pomatoschistus microps* in a French lagoon. J. Fish Biol. **57**: 382–390.

Somarakis, S., Kostikas, I., and Tsimenides, N. 1997. Fluctuating asymmetry in the otoliths of larval fish as an indicator of condition: conceptual and methodological aspects. J. Fish Biol. **51**(Suppl. A): 30–38.

Tesch, F.-W. 2003. The eel. 5th ed. Blackwell Science, Oxford.

Tolonen, A., Palavuo, M., Muje, P., and Rita, H. 2002. Energy density and fecundity in subarctic European whitefish (*Coregonus lavaretus* (L.)) infected by *Diphyllobothrium ditremum* plerocercoids. Arch. Hydrobiol. Spec. Issue Adv. Limnol. **57**: 527–535.

Toms, J.D., and Lesperance, M.L. 2003. Piecewise regression: a tool for identifying ecological thresholds. Ecology, **84**: 2034–2041.

Vallisneri, M., and Scapolatempo, M. 2000. The population patterns and reproductive biology of *Engraulis encrasicolus* L. (Engraulidae, Teleostei) in the northern and middle Adriatic Sea. Boll. Soc. Adriat. Sci. Trieste, **80**: 81–86.

Wedekind, C., and Müller, R. 2004. Parental characteristics versus egg survivnl: towards an improved genetic management in the supportive breeding of lake whitefish. Ann. Zool. Fenn. **41**: 105–115.

Wilson, J.P.F., and Pitcher, T.J. 1984. Age determination and growth of the pollan, *Coregonus autumnalis pollan* Thompson, of Lough Neagh, Northern Ireland. J. Fish Biol. **24**: 151–163.

Winters, G.H. 1971. Fecundity of the left and right ovaries of Grand Bank capelin (*Mallotus villosus*). J. Fish. Res. Board Can. **28**: 1029–1033.

© 2005 NRC Canada

Body size, not other morphological traits, characterizes cascading effects in fish assemblage composition following commercial netting

C.A. Layman, R.B. Langerhans, and K.O. Winemiller

Abstract: Traits used to group species and generalize predator–prey interactions can aid in constructing models to assess human impacts on food webs, especially in complex, species-rich systems. Commercial netting has reduced populations of large-bodied piscivores in some lagoons of a Venezuelan floodplain river, and cascading effects result in distinct prey fish communities in netted and unnetted lagoons. In 2002 and 2003, we sampled assemblages of prey fishes in netted and unnetted lagoons and tested whether fish size and (or) other morphological characteristics were associated with differences in assemblage composition. In both years, prey fish assemblages in netted lagoons were dominated numerically by larger species. We used geometric morphometric methods to test for a relationship between species morphological characteristics and found that neither overall morphological ordination nor specific morphological traits could be used to distinguish among assemblages. Thus, size was the only variable that was useful in explaining differences in assemblage composition. Even in this species-rich river with a complex food web, size-structured predator–prey interactions apparently influence community-level patterns and can be used to characterize human impacts.

Résumé : Les caractéristiques utilisées pour regrouper les espèces et pour généraliser les interactions prédateurs–proies peuvent servir à construire des modèles d'évaluation des impacts anthropiques sur les réseaux alimentaires, particulièrement dans les systèmes complexes, riches en espèces. La pêche commerciale au filet a réduit les populations des piscivores de grande taille dans certains lagons de la plaine de débordement d'une rivière du Venezuela et les effets en cascade qui s'en sont suivis ont donné des communautés distinctes de poissons proies dans les lagons soumis à la pêche et dans ceux qui ne le sont pas. En 2002 et 2003, nous avons échantillonné des peuplements de poissons proies dans des lagons exploités et non exploités et vérifié s'il existe une association entre la taille et (ou) d'autres caractéristiques morphologiques des poissons et les différences de composition des peuplements. Durant les deux années, les peuplements de poissons proies dans les lagons exploités étaient dominés numériquement par des espèces plus grandes. Des méthodes morphométriques géométriques nous ont servi à chercher à découvrir une relation entre les caractéristiques morphologiques des espèces; nous n'avons trouvé ni d'ordination globale morphologique, ni de caractéristiques morphologiques spécifiques qui permettent de distinguer les peuplements. La taille est donc la seule variable utile pour expliquer les différences de composition des peuplements. Même dans cette rivière riche en espèces et à réseau alimentaire complexe, les interactions prédateurs–proies reliées à la taille semblent influencer les patrons au niveau de la communauté et peuvent servir à caractériser les impacts anthropiques.

[Traduit par la Rédaction]

Introduction

Predicting effects of human activity on ecological interactions and ecosystem function is one of the most important challenges facing ecologists. Species exploitation, species introductions, and habitat alteration all can lead to changes in food web structure, and understanding these changes is necessary to mitigate negative impacts of human activities. Perturbations propagate through multiple trophic and nontrophic pathways rendering it difficult to predict impacts, es-

Received 3 January 2005. Accepted 29 June 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 8 November 2005.
J18487

C.A. Layman.[1] Department of Ecology and Evolutionary Biology, Yale University, P.O. Box 208106, New Haven, CT 06520-8106, USA.
R.B. Langerhans. Department of Biology, Campus Box 1137, Washington University, St. Louis, MO 63130-4899, USA.
K.O. Winemiller. Section of Ecology and Evolutionary Biology, Department of Wildlife and Fisheries Sciences, 210 Nagle Hall, Texas A&M University, College Station, TX 77843-2258, USA.

[1]Corresponding author (CAL1634@yahoo.com).

 doi: 10.1139/F05-183 © 2005 NRC Canada

pecially in complex food webs (Yodzis 2000; Wootton 2001; Relyea and Yurewicz 2002). Yet, modeling effects of human-induced perturbations is essential to guide conservation and management efforts (Chapin et al. 2000; McCann 2000).

Grouping species according to traits, such as size, morphology, or behavior, is one means to simplify species-rich communities, and sometimes provides better predictive capabilities than analyses performed at higher levels of taxonomic resolution. For example, morphological traits are a primary component of "plant functional groups", classifications used to simplify complex plant communities, which have been especially useful for predicting ecosystem- and community-level responses to local and global environmental change (Lavorel et al. 1997; Smith et al. 1997; Dyer et al. 2001). Body size influences population and community responses to perturbations in species-rich arthropod food webs (Dial and Roughgarden 1995; Spiller and Schoener 2001; Schoener et al. 2002). If phenotypic traits can be used to assess ecological responses to perturbations in a broad range of communities, then trait classifications may be a primary tool for assessing anthropogenic impacts on food webs.

Net fishing is one of the most common human influences in tropical inland waters, and can cause major changes in fish communities (Goulding 1980; Bayley and Petrere 1989; Crisman et al. 2003). Piscivore introductions have been shown to substantially alter prey assemblages in tropical lentic systems (Zaret 1979; Kaufman 1992; Crisman et al. 2003), but there have been few studies that examine effects following piscivore removal. In the Río Cinaruco, Venezuela, netters substantially reduce population sizes of large-bodied piscivores in some lagoons of the floodplain landscape. We previously simulated commercial netting effects by excluding large-bodied piscivores on sandbank habitats of the river (exclusion areas ~500 m^2). Piscivore exclusion resulted in shifts in assemblage composition, indicating effects of large piscivores on medium-sized fishes at lower trophic levels (Layman and Winemiller 2004). Assemblage differences were best characterized by the body size of prey taxa, suggesting that phenotypic characteristics might be useful in predicting landscape-scale effects of commercial netting.

We tested the utility of phenotypic traits in characterizing differences in fish assemblages of netted and unnetted lagoons. We specifically assessed whether, as suggested by experimental manipulations, body size could be used to generalize assemblage differences following piscivore removal from lagoons. Second, because body morphology is related to ecological attributes (e.g., vulnerability to predators, swimming performance, feeding behavior) in many fish taxa (e.g., Keast and Webb 1966; Winemiller 1991; Wainwright and Richard 1995), we examined whether morphological traits of prey species could characterize netting effects at the landscape scale. We especially were interested in identifying traits (e.g., relative size of the caudal peduncle region) that may reflect the ability of prey to avoid or escape predators (e.g., Walker 1997; Langerhans et al. 2004, 2005). We examined a subset of the overall food web, i.e., a food web module (sensu Holt 1997), which includes the most important prey species of large-bodied piscivores. Our objectives were to (*i*) describe differences in fish assemblage structure between netted and unnetted lagoons within this food web module and (*ii*) investigate whether prey size and (or) other morphological characteristics can be used to generalize these differences.

Materials and methods

Study site

The study was conducted in the Río Cinaruco, a blackwater, floodplain river in southwestern Venezuela (6°32′N, 67°24′W). The river has a forested riparian zone with open grassland dominating the drainage basin. The river supports at least 280 fish species that span a wide range of ecological attributes and life history strategies (Langerhans et al. 2003; Arrington et al. 2005; Layman and Winemiller 2005). The river has a strongly seasonal hydrology with water levels typically fluctuating >5 m during an annual hydroperiod. Floodplain lagoons (~1–30 km^2) are connected to the river by varying degrees. During the wet season (June–October), lagoons are broadly connected to the main channel, and dispersal of organisms is extensive. During the dry season (January–April), most lagoons become partially isolated water bodies with restricted connections to the river channel (width of connections at lagoon mouths ~1–100 m). During the dry season, species interactions, predation in particular, intensify as densities of aquatic organisms increase with falling water levels (Jepsen et al. 1997; Rodríguez and Lewis 1997; Layman and Winemiller 2004).

During the dry season when water levels are low and fish densities high, some lagoons of the Cinaruco floodplain are exploited by commercial net fishers. Netters use long beach seines (~300 m in length, mesh size ~20 cm) to harvest large-bodied fishes. The seine is deployed in a broad semicircle using a small boat and then pulled onto shore. We classified lagoons a priori as either netted or unnetted based on visual monitoring throughout the dry seasons (January–April) of 2002 and 2003. Evidence of netting activity was direct observation of either netters or piles of discarded carcasses from the fish by-catch (e.g., *Hoplias malabaricus*, *Geophagus* spp.) on lagoon shorelines. Each lagoon was checked at least weekly for evidence of recent netting activity. Lagoons classified as "netted" had evidence of netting on at least five occasions during 2002 or 2003. Lagoons classified as "unnetted" were those in which we never observed any evidence of netting activity. Seven lagoons in 2002 (four unnetted, three netted) and eight in 2003 (five unnetted, three netted) met these criteria and were included in this study. None of the lagoons used was netted in one year and unnetted in the other. There were no differences between netted and unnetted lagoons in area (*t* test, $t = 0.66$, $p = 0.53$), average depth ($t = 0.58$, $p = 0.58$), maximum depth ($t = 1.6$, $p = 0.16$), or average transparency ($t = 1.7$, $p = 0.13$), suggesting that patterns reported in this study are not due to differences in lagoon physical characteristics. Lagoon accessibility largely determined netting status, i.e., netters primarily fished lagoons that were adjacent to roads.

Netters target high-value fish species, including the most common large-bodied piscivores (peacock cichlids (*Cichla orinocensis* and *Cichla temensis*) and a characiform (*Hydrolycus armatus*)). Lagoons are never depleted com-

© 2005 NRC Canada

pletely of piscivores because of net avoidance and immigration from the main river channel, but catch-per-unit-effort (CPUE) estimates of *Cichla* spp. and *H. armatus* in netted and unnetted lagoons suggest that population sizes may be reduced 50% or more by netters. Based on standardized hook-and-line fishing (the most effective methodology to capture *Cichla*), an average of 6.0 *Cichla* individuals were collected per 100 casts in unnetted lagoons compared with <2.4 in netted lagoons (CPUE data summed for 2002 and 2003, total casts = 4856). In standardized gillnet sampling (a more effective method of capturing *H. armatus*), an average of 6.2 *H. armatus* were collected in 24-h sampling periods in unnetted lagoons compared with 2.5 in netted lagoons (total gillnetting hours = 2736).

Fish sampling

Fish communities were sampled by cast-netting at the end of the dry season (April) in 2002 and 2003. Prey taxa most commonly consumed by large-bodied piscivores (Jepsen et al. 1997; Winemiller et al. 1997) are collected efficiently by cast-netting, and this methodology (relative to seining, gillnetting, etc.) was likely to reflect differences in prey fish assemblage structure among netted and unnetted lagoons. In doing so, we were targeting a specific food web module, a subset of interacting species from a larger food web (sensu Holt 1997). Samples were obtained using a 244-cm cast net (mesh size 6.3 mm) thrown from a small boat. All sites were adjacent to woody debris along lagoon shorelines at depths of 40–125 cm. Sites were chosen haphazardly in each lagoon, a sampling design intended to reflect lagoon-scale patterns and not site-specific characteristics (sites per lagoon 3.4 ± 0.8). Three consecutive throws were made with the cast net at each site (sampling an area of ~4.5 m^2) and all fishes were identified to species, enumerated, measured to the nearest 1.0 mm standard length (SL), and released into the lagoon. Voucher specimens of each species were archived in the Museo de Ciencias Naturales at UNELLEZ, Guanare, Venezuela, and the Texas Cooperative Wildlife Collection, College Station, Texas.

Data analysis

For univariate comparisons, *t* tests were employed when assumptions of normality and homogeneity of variance were met and the Mann–Whitney *U* test when they were not. Nonmetric multidimensional scaling (MDS), using the Primer v5.0 statistical package (Clarke and Gorley 2001), was used to compare fish assemblage similarity or dissimilarity based on relative abundances of individual taxa. MDS constructs a two-dimensional ordination in a manner that best represents relationships among samples in a similarity matrix (Field et al. 1982; Clarke and Warwick 2001). In ordination plots, the relative distance between points reflects the dissimilarity of species composition in those samples. Similarity matrices were calculated with the Bray–Curtis similarity index (Bray and Curtis 1957). We conducted a nested multivariate analysis of variance (MANOVA) using the two MDS axes as dependent variables to test for effects of netting regime (netted versus unnetted) and lagoons nested within netting regime on species composition of samples. To compare size structure of assemblages based on all individuals collected, data were pooled for netted and unnetted lagoons for 2002 and 2003 (each year separately). A Mann–Whitney rank sum tested for differences in overall length–frequency distributions for both 2002 and 2003.

To obtain morphometric data, we captured a lateral image of the left side of three adult individuals for each species using a digital camera (Sony DSC-S30) mounted on a tripod. The size of individuals used for each species was ±1 SD of the mean size of all individuals of that species collected over 2 years of the study. Individuals used in the analysis were collected previously from the Río Cinaruco, fixed in 10% formalin, preserved in 70% alcohol, and catalogued at the Texas Cooperative Wildlife Collection, College Station, Texas. We digitized 12 landmarks on each image using tpsDig software (Rohlf 2003) for geometric morphometric analysis. Location of landmarks and examples illustrating the range of interspecific variation among fish species in body size and shape are depicted in Fig. 1.

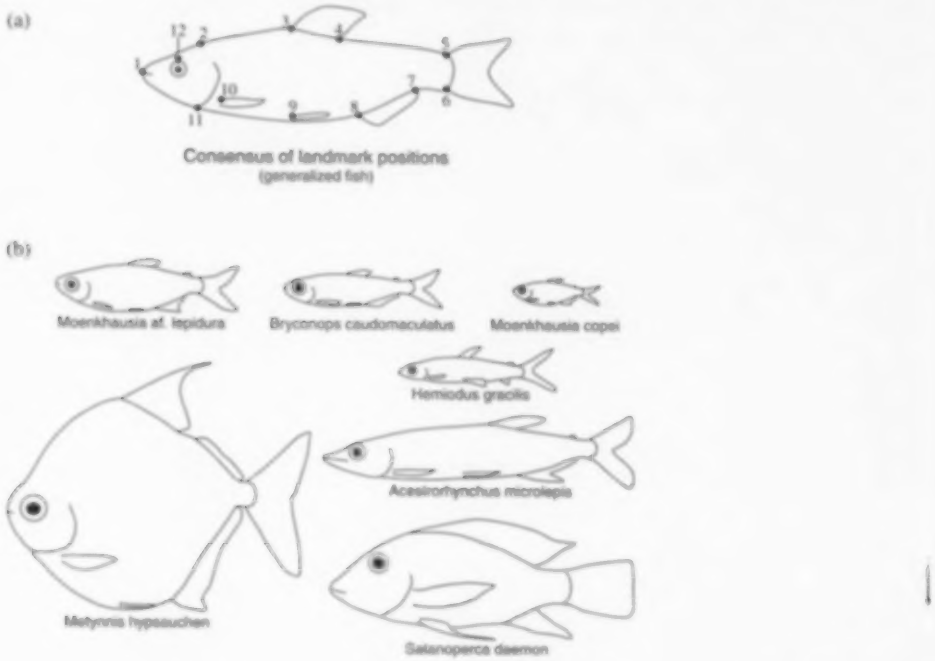
We conducted a relative warp analysis of superimposed landmark coordinates using tpsRelw software (Rohlf 2003). For more information on relative warp analysis and other geometric morphometric techniques, see Bookstein (1991), Rohlf and Marcus (1993), Marcus et al. (1996), and Zelditch et al. (2004). Essentially, relative warp analysis is a principal components analysis of the covariance matrix of the aligned specimens (i.e., rotated, translated, and scaled landmark coordinates). This procedure produces multiple morphological axes (i.e., orthogonal multivariate shape dimensions) in a manner that best explains variance in body shape among specimens. Each relative warp axis represents a set of specific morphological characteristics, allowing particular morphological attributes of species to be analyzed directly. We calculated the average score on each relative warp (n = 20) for each species. Because superimposition methods of geometric morphometrics scale specimens to a common centroid size, size differences among species are removed from the analysis, permitting an evaluation of morphology largely independent of size.

We evaluated three questions. (*i*) Do morphologically similar species exhibit similar patterns of abundance in netted or unnetted lagoons? (*ii*) Can any particular morphological axis (i.e., multivariate description of shape variation) be used to differentiate abundance of species in netted or unnetted lagoons? (*iii*) Considered simultaneously, does body size or shape better characterize assemblage differences? To answer these questions, we quantified CPUE (i.e., mean abundance of individuals per sample) differences among netted and unnetted lagoons ($CPUE = CPUE_{netted} - CPUE_{unnetted}$) for each species and evaluated body shape variation among species using relative warp analysis and MDS. Because CPUE values for each species were repeatable across years (r = 0.71, p = 0.0003), we pooled data across years to estimate CPUE.

For the first question, we constructed a two-dimensional morphospace representing similarity or dissimilarity in body morphology of all species using MDS. These two axes were generated based on a Bray–Curtis similarity index of relative warp scores. Using these two axes, we conducted a canonical correlation analysis to test for a multivariate relationship between body shape and CPUE. This analysis addressed

© 2005 NRC Canada

Fig. 1. Landmarks used for morphometric analyses and illustration of variation in size and morphology of fish assemblages. (*a*) Consensus landmark configuration depicting average position of the 12 digitized landmarks; (*b*) seven fish species illustrating variability of body forms observed within this food web module. The relative size of species (mean size of individuals of each species collected in this study) is drawn to scale.



whether morphologically similar species exhibited similar patterns of abundance.

To answer our second question, we tested for a correlation between CPUE and each of the 20 relative warps. We used Bonferroni-adjusted p values for multiple comparisons to test for significance.

Our third question addressed the utility of using body size and body morphology to characterize species abundance patterns associated with commercial netting. Based on results of a previous study (Layman and Winemiller 2004), as well as results from the assemblage analysis of this study (see Results section), we placed each species into one of two size classes (<40 and >40 mm SL). We performed a general linear model evaluating differences in species abundances between netted and unnetted lagoons (CPUE, the response variable) as predicted by size class and the two morphological axes generated by MDS. We tested for interactions among effects and found no significant interaction and thus excluded all interactions in the final model.

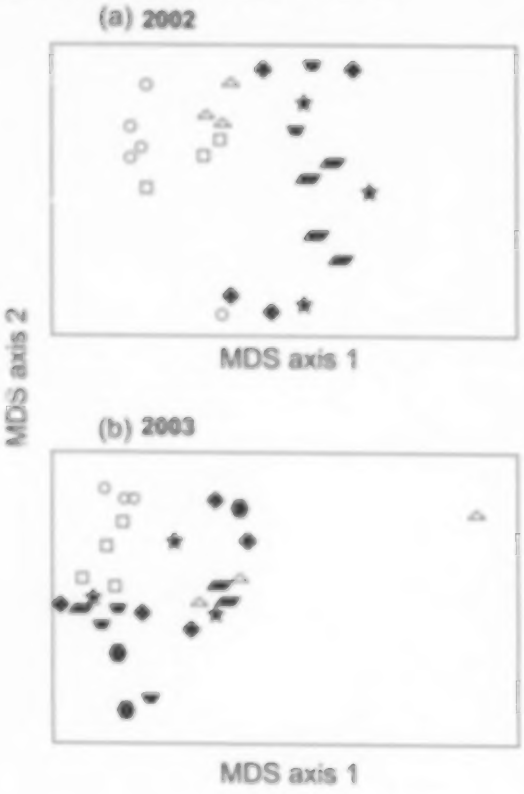
Results

A total of 2633 individual fishes representing 40 species were collected using the standardized cast-netting protocol. Twenty of the 40 taxa were collected rarely (five or fewer individuals collected in all samples from both years) and were excluded from assemblage and morphological analyses. Abundance of fishes collected per site was significantly higher in netted lagoons in 2003 (t test, $p = 0.011$; mean ± 1 SD: netted = 44 ± 35, unnetted = 17 ± 15) but not in 2002 (Mann–Whitney U test, $p = 0.34$; netted = 85 ± 54, unnetted = 76 ± 85). Species density (i.e., number of species collected in a standardized sample (sensu Gotelli and Colwell 2001)) also was significantly higher in netted lagoons in 2003 (t test, $p = 0.042$; netted = 5.8 ± 3.5, unnetted = 3.6 ± 1.8) but not in 2002 (t test, $p = 0.14$; netted = 6.8 ± 1.6, unnetted = 5.6 ± 2.1). Taxa were variable in size (11–257 mm SL) and morphology (see Fig. 1). Taxa collected included pelagic characids and hemiodids (e.g., *Moenkhausia* af. *lepidura*, *Hemiodus gracilis*), benthic cichlids (e.g., *Satanoperca daemon*), other demersal species (e.g., *Cyphocharax oenas*), a loracariid algivore (*Rineloricaria* spp.), and deep-bodied pelagic granivores (e.g., *Metynnis hypsauchen*).

MANOVA revealed that species composition significantly differed between netted and unnetted lagoons in 2002 ($F_{[2,16]} = 32.23$, $p < 0.0001$) and 2003 ($F_{[2,18]} = 4.28$, $p = 0.03$) and among lagoons nested within netting regime in 2003 ($F_{[12,36]} = 2.25$, $p = 0.03$) but not in 2002 ($F_{[10,32]} = 1.26$, $p = 0.29$) (Fig. 2). Thus, although differences in composition of netted and unnetted lagoon sites were significant during both years, they were more distinct in 2002 (i.e., clearer separation in ordination space, less variation within netting regimes; see Fig. 2). During both years, netted lagoon sites were dominated numerically by *M.* af. *lepidura* (2002, 44% of individuals collected; 2003, 70%). In unnetted lagoons, *M.* af. *lepidura* accounted for only 3% (2002) and <1% (2003) of individuals collected. *Moenkhausia copei* accounted for 71% (2002) and 40% (2003) of fishes collected in unnetted la-

© 2005 NRC Canada

Fig. 2. Differences in species assemblage composition as reflected by nonmetric MDS: (*a*) 2002; (*b*) 2003. MANOVA revealed significant differences in assemblage composition between netted and unnetted lagoons in both years. Each symbol represents a different lagoon; open symbols are sites in netted lagoons and solid symbols are sites in unnetted lagoons.



goons and 10% in both 2002 and 2003 in netted lagoons. Abundance of these two species largely accounted for relative positions of the sites in the MDS ordination in both years.

We found significant differences in overall size distribution of fishes, regardless of species (i.e., individual-level analysis), between netted and unnetted lagoons for both years (Mann–Whitney U test, $p < 0.001$, both years) (Fig. 3). Unnetted lagoons were dominated by fishes <40 mm SL. This was largely accounted for by the two most common species in unnetted lagoon samples, *M. copei* (SL ± SD = 35.5 ± 3.7 mm) and *Hemigrammus* sp. (SL = 16.8 ± 1.0 mm). In netted lagoons, there was a peak in both years in fishes 61–70 mm, accounted for largely by *M.* aff. *lepidura* (66.9 ± 5.1 mm). Other larger species, including *Bryconops caudomaculatus*, *Acestrorhynchus microlepis*, and *Acestrorhynchus minimus*, were also more commonly collected in netted lagoons. Differences in assemblage composition and size structure were more distinct in 2002 than in 2003; this could be attributed to apparent reduced netting activity during January–February 2003, which could have resulted in less distinct divergence in faunal composition.

In morphological analyses, canonical correlation analysis revealed no significant association between body morphology and CPUE ($F_{[2,17]} = 0.13$, $p = 0.88$). Although species exhibited distinct differences in morphological features, these differences or similarities were not correlated with abundance patterns in netted or unnetted lagoons. After Bonferroni adjustment (i.e., using a significance level of $p = 0.0025$), no correlations among relative warps ($n = 20$) and CPUE were significant (Table 1) (the first two relative warps accounting for 72.6% of the total morphological variance are depicted in Fig. 4). One relative warp (relative warp 20, explaining only 0.03% of morphological variance) was highly correlated with CPUE before Bonferroni correction ($R = 0.56$, $p = 0.011$). Visual inspection suggested that this relative warp described subtle morphological differences between species <40 and >40 mm SL. We tested this hypothesis using a t test and found significant differences in relative warp 20 values between the two size classes of fish ($p = 0.0015$). Thus, the only morphological attribute that characterized ecological patterns between netted and unnetted lagoons primarily described differences between these two size classes of fish.

In a general linear model examining effects of size class and morphology (i.e., the MDS axes) on CPUE, we found that size class significantly characterized species abundance patterns ($F_{[1,16]} = 4.85$, $p = 0.043$) but that neither morphological axis was associated with abundance patterns (axis 1, $F_{[1,16]} = 0.009$, $p = 0.925$; axis 2, $F_{[1,16]} = 1.65$, $p = 0.218$). Again, we found no evidence that morphological features could be used to characterize differences in netted and unnetted lagoons, whereas a simple size-class categorization could be used to assess effects of commercial netting. Further, the analysis had adequate statistical power to detect putative effects of morphology on CPUE (statistical power of 0.97 assuming an effect size equivalent to that of the size-class factor). This species-level analysis indicated that species >40 mm SL exhibited greater abundance in netted lagoons and that species <40 mm SL were more abundant in unnetted lagoons. Thus, differences in length distributions revealed by individual-level analysis (Fig. 3) were not solely due to differences exhibited by numerically dominant species.

Discussion

Body size, but not other morphological traits, was associated with differences in prey assemblage composition among netted and unnetted lagoons. These results are consistent with experimental manipulations demonstrating a size-based prey response to piscivore exclusion in this system (Layman and Winemiller 2004) and suggest that experimental results "scale up" to characterize landscape-level patterns. Body size has been used similarly to model human impacts on marine fishing stocks (Rice and Gislason 1996; Pauly et al. 1998; Shin and Cury 2001) and to predict phytoplankton community shifts in response to nutrient and food web manipulations (Cottingham 1999; Klug and Cottingham 2001). Size-structured predator–prey interactions are fundamental for understanding aquatic food web structure, and our results suggest that size can be used to assess fishing effects even within highly diverse, reticulate food webs.

© 2005 NRC Canada

Fig. 3. Length–frequency histograms showing different size structures of assemblages in (*a*) netted and (*b*) unnetted lagoons. Bars represent proportion of total fishes collected in each size category: solid bars, 2002; open bars, 2003.

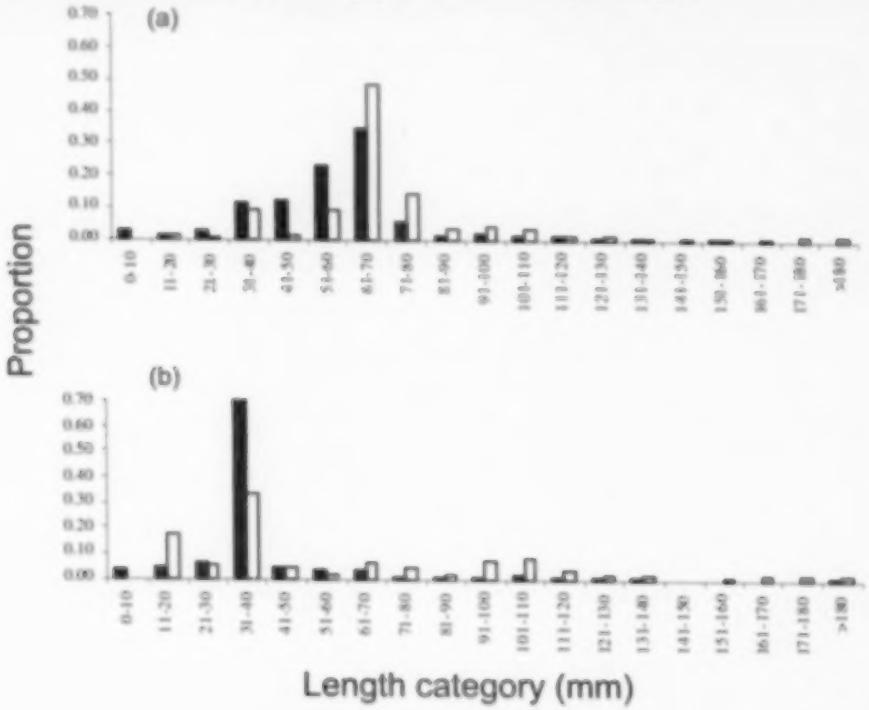


Table 1. Descriptive information and correlation statistics for the first 10 relative warps (explaining ~99% of the morphological variance).

Relative warp	Percent variance explained	Cumulative percent variance explained	Correlation with CPUE	
			r	*p*
1	51.49	51.49	0.01	0.971
2	21.09	72.58	0.04	0.874
3	12.14	84.72	0.06	0.812
4	7.59	92.31	0.04	0.859
5	2.19	94.50	0.15	0.539
6	1.61	96.11	0.10	0.679
7	1.15	97.26	0.21	0.384
8	0.72	97.98	0.00	0.993
9	0.46	98.44	0.24	0.303
10	0.37	98.81	0.02	0.949

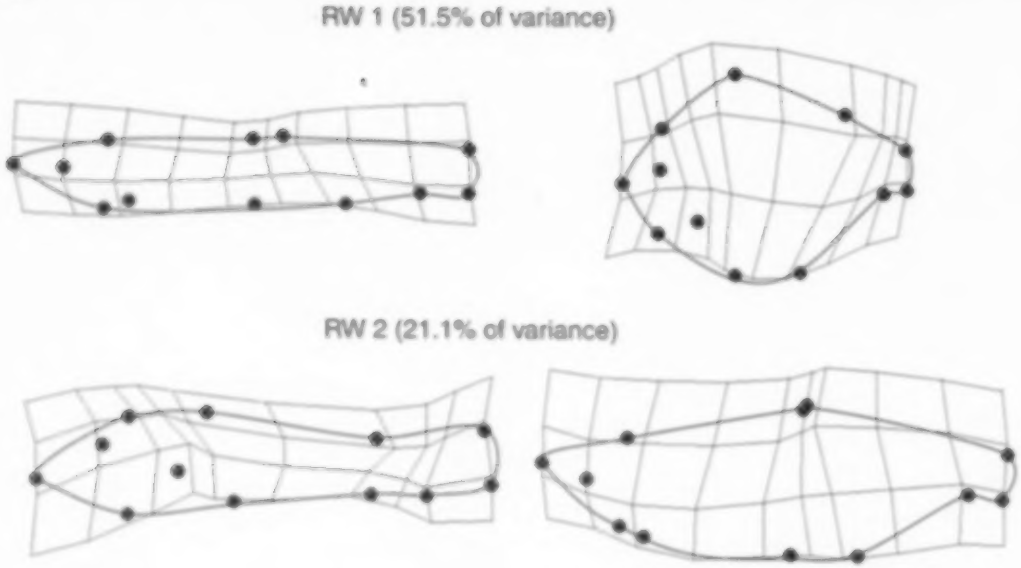
Note: None of the correlations between relative warps ($n = 20$) and ΔCPUE (i.e., the difference in CPUE) was significant using Bonferroni correction for multiple comparisons. With Bonferroni adjustment, we used a significance level of $p = 0.0025$.

Following other studies of lake- or lagoon-scale patterns of community structure (Rahel 1984; Tonn et al. 1990; Rodríguez and Lewis 1997), we employed a comparative-based approach and analyzed patterns based on an underlying variable. Rodríguez and Lewis (1997) demonstrated that a suite of abiotic (e.g., lagoon morphology, water transparency) and biotic (e.g., piscivore abundance) variables determined community structure in lagoons of the Río Orinoco, whereas we based our comparison a priori on a single categorical variable (netting history). Together, these studies demonstrate that piscivory is an important factor structuring fish assemblages in floodplain lagoons. Similar to the study of Rodríguez and Lewis (1994), we suggest that species-specific differences in vulnerability to piscivores strongly influence assemblage composition during the dry season in tropical floodplain lagoons.

The Río Cinaruco is characterized by a compressed food web in which all piscivores seem to exploit prey that both feed low in the food web (i.e., on algivores and detritivores) and are optimally sized (Layman et al. 2005*a*). At the end of the dry season (April), algivores and detritivores are largely depleted from the potential prey fish community (Jepsen et al. 1997; Layman et al. 2005*b*), but the present study suggests that piscivores continue to exploit optimally sized prey even as they are forced to feed on prey positioned higher in the food web (e.g., on omnivorous *Moenkhausia* and *Brycon-ops* spp.). Profitability (energy or biomass ingested in relation to capture and handling efficiencies) of a prey resource is typically greatest at intermediate to large prey sizes, although consumption of specific prey is a function of prey density, behavior, sensory ability, and predator capture and handling efficiency (Sih and Moore 1990; Sih and Christensen 2001; Scharf et al. 2002). By preferentially consuming larger individuals to maximize profitability, piscivores may allow smaller prey to dominate fish assemblages in Cinaruco lagoons. When commercial netting re-

© 2005 NRC Canada

Fig. 4. Thin-plate spline transformations of landmark coordinates depicting morphological characteristics described by the first two relative warps (RW) (accounting for 72.6% of the morphological variance). Low values of relative warps are on the left and high values are on the right.



duces densities of large-bodied piscivores, larger prey fishes dominate this module of the food web. Such size-based differences in fish assemblages are consistent with well-documented size-structured patterns in planktivore–zooplankton–phytoplankton interactions in lotic systems (Brooks and Dodson 1965; Carpenter and Kitchell 1993; Rodríguez et al. 1993).

Morphological traits could prove useful for describing differences in assemblage composition resulting from the influence of prey selection by predators and (or) the ability of prey to escape or avoid predators; we did not find evidence for either of these possibilities. First, if prey selection by predators is relatively unhindered by prey morphological traits, morphology would not be expected to be useful in predicting assemblage-level differences. Large-bodied piscivores in the Río Cinaruco feed on a variety of prey items with greatly varying morphologies, including taxa with defensive spines (*Pimelodella* spp.), armour (*Scorpiodoras* spp., *Leptodoras* sp.), and cryptic morphologies (*Microglanis* sp.) (C.A. Layman, unpublished data). But even with increases in "effective" body size because of spines and other morphological characteristics, body depths of >97% of individuals sampled in this study would not exceed gape limits of most adult large-bodied piscivores, and thus, morphology should not significantly limit prey choice. Prey choice of aquatic predators is often passive (Sih and Moore 1990; Juanes and Conover 1994), especially for species feeding on mobile taxa such as fishes (Sih and Christensen 2001). For large piscivores of Cinaruco lagoons, encounter frequency and prey density may be relatively more important than constraints imposed by prey morphologies for prey selection, especially in the peak dry season when large algivore and detrivores are greatly reduced in abundance.

Additionally, we found no morphological traits related to predator avoidance or escape ability that were correlated with assemblage-level differences. This is likely due to the phylogenetically and morphologically diverse group of prey species included in this study. Behavioral avoidance and escape mechanisms likely vary substantially among the suite of taxa studied, with the underlying morphologies supporting these mechanisms being equally diverse. For example, we have identified within-species morphological differences that consistently differ among individuals in netted and unnetted lagoons, but these morphological differences are unique for separate species (C.A. Layman and R.B. Langerhans, unpublished data). There have likely been multiple evolutionary solutions to predator avoidance and escape in this system, and we could identify no general morphological pattern across all species examined.

Discussion continues as to whether lumping or grouping species into "kinds of organisms", trophospecies, or functional groups is useful when modeling food webs (Yodzis and Winemiller 1999; Schmitz and Sokol-Hessner 2002; Chalcraft and Resetarits 2003). Our study revealed that fish size, but not other morphological characteristics, could be used to group diverse prey taxa to predict assemblage changes following a specific perturbation, i.e., netting of large-bodied piscivores. Consistent results from experimental manipulations and landscape-scale patterns provide strong evidence of the impacts of piscivore removal. Even in this species-rich, tropical food web, size-structured interactions yield large-scale fish assemblage patterns that can be used to assess human impacts.

Acknowledgments

Don Taphorn of Universidad de Los Llanos Occidentales (UNELLEZ) assisted with logistics and fish identification. Fish collections were made with fishing permits 0439 and 0486 issued by the Servicio Autonomo de los Recursos

© 2005 NRC Canada

Pesqueros y Acuicolas of Venezuela. Edgar Pelaéz, Glenn Webb, Jim Marzoula, and Carol Marzoula provided invaluable logistical support through the Cinaruco River Fishing Club and Tour Apure, Guanare. D. Albrey Arrington provided valuable comments on earlier versions of the manuscript. This work was funded by an US Environmental Protection Agency Science to Achieve Results Graduate Fellowship, William "Bill" Baab Conservation Fellowship, Texas A&M Regents and Tom Slick Fellowships, and National Science Foundation grants DEB-0411978 and DEB-0089834.

References

Arrington, D.A., Winemiller, K.O., and Layman, C.A. 2005. Community assembly at the patch scale in a species-rich tropical river. Oecologia, **144**.

Bayley, P.B., and Petrere, M.J. 1989. Amazon fisheries: assessment methods, current status and management options. Can. J. Fish. Aquat. Sci. **46**: 385–398.

Bookstein, F.L. 1991. Morphometric tools for landmark data. Cambridge University Press, Cambridge, UK.

Bray, J.R., and Curtis, J.C. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. **27**: 325–349.

Brooks, J.L., and Dodson, S.I. 1965. Predation, body size, and composition of plankton. Science (Wash., D.C.), **150**: 228–235.

Carpenter, S.R., and Kitchell, J.F. (*Editors*). 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Chalcraft, D.R., and Resetarits, W.J.J. 2003. Mapping functional similarity of predators on the basis of trait similarities. Am. Nat. **162**: 390–402.

Chapin, F.S.I., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., and Díaz, S. 2000. Consequences of changing biodiversity. Nature (Lond.), **405**: 234–242.

Clarke, K.R., and Gorley, R.N. 2001. Primer v5: user manual/tutorial. Primer-E Ltd., Plymouth, UK.

Clarke, K.R., and Warwick, R.M. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Primer-E Ltd., Plymouth, UK.

Cottingham, K.L. 1999. Nutrients and zooplankton as multiple stressors of phytoplankton communities: evidence from size structure. Limnol. Oceanogr. **44**: 810–827.

Crisman, T.J., Chapman, L.J., Chapman, C.A., and Kaufman, L.S. 2003. Conservation, ecology, and management of African fresh waters. University Press of Florida, Gainesville, Fla.

Dial, R., and Roughgarden, J. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. Ecology, **76**: 1821–1834.

Dyer, A.R., Goldberg, D.E., Turkington, R., and Sayre, C. 2001. Effects of growing conditions and source habitat on plant traits and functional group definition. Funct. Ecol. **15**: 85–95.

Field, J.G., Clarke, K.R., and Warwick, R.M. 1982. A practical strategy for analyzing multi-species distribution patterns. Mar. Ecol. Prog. Ser. **8**: 37–53.

Gotelli, N.J., and Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. **4**: 379–391.

Goulding, M. 1980. The fishes and the forest. University of California Press, Berkeley, Calif.

Holt, R.D. 1997. Community modules. *In* Multitrophic interactions in terrestrial systems. *Edited by* A.C. Gange and V.K. Brown. Blackwell Science, Oxford, UK. pp. 333–351.

Jepsen, D.B., Winemiller, K.O., and Taphorn, D.C. 1997. Temporal patterns of resource partitioning among *Cichla* species in a Venezuelan blackwater river. J. Fish Biol. **51**: 1085–1108.

Juanes, F., and Conover, D.O. 1994. Piscivory and prey size selection in young of-the-year bluefish: predator preference or size-dependent capture success? Mar. Ecol. Prog. Ser. **114**: 59–69.

Kaufman, L. 1992. Catastrophic change in species-rich freshwater ecosystems: the lessons of Lake Victoria. Bioscience, **42**: 846–58.

Keast, A., and Webb, D. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. **23**: 1845–1874.

Klug, J.L., and Cottingham, K.L. 2001. Interactions among environmental drivers: community responses to changing nutrients and dissolved organic carbon. Ecology, **82**: 3390–3403.

Langerhans, R.B., Layman, C.A., Langerhans, A.K., and DeWitt, T.J. 2003. Habitat-associated morphological divergence in two neotropical fish species. Biol. J. Linn. Soc. **80**: 689–698.

Langerhans, R.B., Layman, C.A., Shokrollahi, A.M., and DeWitt, T.J. 2004. Predator-driven phenotypic diversification in *Gambusia affinis*. Evolution, **58**: 2305–2318.

Langerhans, R.B., Layman, C.A., and DeWitt, T.J. 2005. Male genital size reflects a tradeoff between attracting mates and avoiding predators in two live-bearing fish species. Proc. Natl. Acad. Sci. **102**(21): 7618–7623.

Lavorel, S., McIntyre, S., Landsberg, J., and Forbes, T.D.A. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends Ecol. Evol. **12**: 474–478.

Layman, C.A., and Winemiller, K.O. 2004. Size-based prey response to piscivore exclusion in a neotropical river. Ecology, **85**: 1311–1320.

Layman, C.A., and Winemiller, K.O. 2005. Patterns of habitat segregation among large fishes in a neotropical floodplain river. Neotrop. Ichthylol. **3**: 103–109.

Layman, C.A., Winemiller, K.O., Arrington, D.A., and Jepsen, D.B. 2005*a*. Body size and trophic position in a diverse tropical food web. Ecology, **86**: 2530–2535.

Layman, C.A., Winemiller, K.O., and Arrington, D.A. 2005*b*. Describing the structure and function of a neotropical river food web using stable isotope ratios, stomach contents, and functional experiments. *In* Dynamic food webs: multispecies assemblages, ecosystem development, and environmental change. *Edited by* J.C. Moore, P. De Ruiter, and V. Wolters. Elsevier/Academic Press, London, UK. In press.

Marcus, L.F., Corti, M., Loy, A., Naylor, G.J.P., and Slice, D.E. 1996. Advances in morphometrics. Plenum Press, New York.

McCann, K.S. 2000. The diversity–stability debate. Nature (Lond.), **405**: 228–233.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. Science (Wash., D.C.), **279**: 860–863.

Rahel, F.J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. Ecology, **65**: 1276–1289.

Relyea, R.A., and Yurewicz, K.L. 2002. Predicting community outcomes from pairwise interactions: integrating density- and trait-mediated effects. Oecologia, **131**: 569–579.

Rice, J., and Gislason, H. 1996. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. ICES J. Mar. Sci. **53**: 1214–1225.

Rodríguez, M.A., and Lewis, W.M., Jr. 1994. Regulation and stability in fish assemblages of neotropical floodplain lakes. Oecologia, **99**: 166–180.

© 2005 NRC Canada

Rodríguez, M.A., and Lewis, W.M., Jr. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. Ecol. Monogr. **67**: 109–128.

Rodríguez, M.A., Magnan, P., and Lacasse, S. 1993. Fish species composition and lake abiotic variables in relation to the abundance and size structure of cladoceran zooplankton. Can. J. Fish. Aquat. Sci. **50**: 638–647.

Rohlf, F.J. 2003. tpsDig. Version 1.38. Department of Ecology and Evolution, State University of New York, Stony Brook, N.Y.

Rohlf, F.J., and Marcus, L.F. 1993. A revolution in morphometrics. Trends Ecol. Evol. **8**: 129–132.

Scharf, F.S., Buckel, J.A., and Juanes, F. 2002. Size-dependent vulnerability of juvenile bay anchovy *Anchoa mitchilli* to bluefish predation: does large body size always provide a refuge? Mar. Ecol. Prog. Ser. **233**: 241–252.

Schmitz, O., and Sokol-Hessner, L. 2002. Linearity in the aggregate effects of multiple predators in a food web. Ecol. Lett. **5**: 168–172.

Schoener, T.W., Spiller, D.A., and Losos, J.B. 2002. Predation on a common *Anolis* lizard: can the food-web effects of a devastating predator be reversed? Ecol. Monogr. **72**: 383–407.

Shin, Y., and Cury, P. 2001. Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. Aquat. Living Resour. **14**: 65–80.

Sih, A., and Christensen, B. 2001. Optimal diet theory: when does it work, and when and why does it fail? Anim. Behav. **61**: 379–390.

Sih, A., and Moore, R.D. 1990. Interacting effects of predator and prey behavior in determining diets. *In* Behavioural mechanisms of food selection. *Edited by* R.N. Hughes. Springer-Verlag, Berlin. pp. 771–796.

Smith, T.M., Shugart, H.H., and Woodward, F.I. (*Editors*). 1997. Plant functional types, their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, UK.

Spiller, D.A., and Schoener, T.W. 2001. An experimental test for predator-mediated interactions among spider species. Ecology, **82**: 1560–1570.

Toon, W.M., Magnuson, J.J., Rask, M., and Toivonen, J. 1990. Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. Am. Nat. **136**: 345–375.

Wainwright, P.C., and Richard, B.A. 1995. Predicting patterns of prey use from morphology of fishes. Environ. Biol. Fishes, **44**: 97–113.

Walker, J.A. 1997. Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape. Biol. J. Linn. Soc. **61**: 3–50.

Winemiller, K.O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecol. Monogr. **61**: 343–365.

Winemiller, K.O., Taphorn, D.C., and Barbarino-Duque, A. 1997. Ecology of *Cichla* (Cichlidae) in two blackwater rivers of southern Venezuela. Copeia, 1997: 690–696.

Wootton, J.T. 2001. Prediction in complex communities: analysis of empirically derived Markov models. Ecology, **82**: 580–598.

Yodzis, P. 2000. Diffuse effects in food webs. Ecology, **81**: 261–266.

Yodzis, P., and Winemiller, K.O. 1999. In search of operational trophospecies in a tropical aquatic food web. Oikos, **87**: 327–340.

Zaret, T.M. 1979. Predation in freshwater communities. *In* Predator–prey systems in fishery management. *Edited by* H. Klepper. Sport Fishing Institute, Washington, D.C. pp. 135–143.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D., and Fink, W.L. 2004. Geometric morphometrics for biologists: a primer. Elsevier/Academic Press, London, UK.

© 2005 NRC Canada

Juvenile salmonid (*Oncorhynchus* spp.) use of constructed and natural side channels in Pacific Northwest rivers

Sarah A. Morley, Patricia S. Garcia, Todd R. Bennett, and Philip Roni

Abstract: Off-channel habitats, critical components in the life histories of Pacific salmonids (*Oncorhynchus* spp.), have become increasingly rare in human-modified floodplains. The construction of groundwater-fed side channels is one approach that has been used in the Pacific Northwest to recreate off-channel habitats. We evaluated the effectiveness of this technique by comparing 11 constructed side channels with paired reference sites (naturally occurring channels fed by mixed groundwater and surface water) in western Washington. While total salmonid densities were not significantly different between channel types, coho salmon (*Oncorhynchus kisutch*) densities were higher in constructed channels and trout densities were higher in reference channels during the winter. Constructed channels were deeper than reference channels and warmer in the winter and cooler in the summer but had lower physical habitat diversity, wood density, and canopy coverage. We did not detect significant differences in water chemistry or invertebrate parameters between channel types. Summer coho density was inversely correlated with minimum daily temperature and with total nitrogen and total phosphorous concentrations. Relative to other stream habitats, both constructed and reference channels supported high densities of juvenile coho salmon during the summer and winter.

Résumé : Les habitats hors du chenal, des composantes essentielles du cycle biologique des salmonidés du Pacifique (*Oncorhynchus* spp.), deviennent de plus en plus rares dans les plaines de débordement modifiées par l'activité humaine. La construction de chenaux latéraux alimentés par la nappe phréatique est l'une des méthodes utilisées dans la région pacifique du nord-ouest pour récréer les habitats hors du chenal. Nous évaluons l'efficacité de cette technique en comparant 11 chenaux latéraux artificiels à des sites appariés (des chenaux d'origine naturelle alimentés par un mélange d'eau phréatique et d'eau de surface) dans l'ouest du Washington. Bien que les densités totales de salmonidés ne soient pas significativement différentes dans les deux types de chenaux, les densités de saumons coho (*Oncorhynchus kisutch*) sont plus élevées dans les chenaux artificiels et les densités de truites plus grandes dans les chenaux témoins en hiver. Les chenaux artificiels sont plus profonds que les chenaux témoins, ils sont plus chauds en hiver et plus frais en été, mais ils possèdent une diversité d'habitat physique, une densité de bois et une couverture d'arbres plus faibles. Nous n'avons pas trouvé de différences significatives de qualité de l'eau, ni de caractéristiques de la faune invertébrée dans les deux types de chenaux. Les densités de saumons coho en été sont en corrélation inverse avec la température journalière minimale et avec les concentrations d'azote et de phosphore totaux. Par comparaison à d'autres habitats de cours d'eau, tant les chenaux artificiels que les chenaux témoins contiennent de fortes densités de jeunes saumons coho durant l'été et l'hiver.

[Traduit par la Rédaction]

Introduction

Off-channel habitats, such as sloughs, side channels, beaver ponds, and other permanently or seasonally flooded areas, are important rearing areas for juvenile salmonids (*Oncorhynchus* spp.; Groot and Margolis 1991). Coho salmon (*Oncorhynchus kisutch*) particularly favor these slow-water habitats, which they typically migrate into following fall freshets (Bustard and Narver 1975; Peterson 1982*a*; Nickelson et al. 1992*a*). In addition to refuge from high flows in the mainstem, off-channel habitats also often provide a less variable temperature regime and a consistent invertebrate food supply (Peterson 1982*b*; Lister and Finnigan 1997). A number of studies have reported that juvenile coho remaining in off-channel habitats to overwinter exhibit higher growth rates relative to coho occupying mainstem habitats (Bustard and Narver 1975; Tschaplinski and Hartman 1983; Swales and Levings 1989).

As rivers were channelized and isolated from their floodplains, riparian areas developed, and hydrologic and sediment regimes were greatly altered by human activities, off-channel habitats were frequently lost. Beechie et al. (1994) estimated that slough habitat has been reduced by more than 50% in the Skagit River Basin of Washington State, and Nickelson et al. (1992*a*) suggest that lack of adequate high

Received 19 January 2005. Accepted 4 July 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 3 November 2005.
J18509

S.A. Morley,[1] P.S. Garcia, T.R. Bennett, and P. Roni. Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112-2097, USA.

[1]Corresponding author (e-mail: sarah.morley@noaa.gov).

 doi: 10.1139/F05-185 © 2005 NRC Canada

quality overwintering habitat (such as off-channel areas) limits coho production on the Oregon coast. These concerns have spurred varied off-channel habitat restoration efforts across the Pacific Northwest, with one common technique being the construction of riverine groundwater side channels (Lister and Finnigan 1997).

Side channels were first constructed in British Columbia in the late 1970s as artificial spawning channels for chum salmon (*Oncorhynchus keta*) (Lister et al. 1980; Bonnell 1991). When later evaluation found that they were also being used as rearing habitat by juvenile coho (Sheng et al. 1990), subsequent channels were built in British Columbia and Washington State specifically targeting this species (Giannico and Hinch 2003). Currently, two west coast coho salmon evolutionarily significant units (ESUs) are listed as threatened under the US Endangered Species Act, two ESUs are candidates for species listing, and one is considered a "species of concern" (NMFS 2003). As federal- and state-sponsored financial assistance for restoration projects has increased, so too has the number of side-channel construction projects (WDFW 1999–2003).

The objective of this study was to evaluate the effectiveness of these constructed groundwater side channels in providing habitat for Pacific salmonids. Although many of these channels were constructed over a decade ago, relatively few studies have examined their long-term success, particularly in relation to juvenile salmonid use. Nor have any studies directly compared these constructed channels with their naturally occurring equivalents. To determine the effectiveness of this restoration technique, we compared physical habitat, temperature regime, water chemistry, and invertebrate and fish use between constructed and naturally occurring side channels. We also investigated what particular features contribute to one channel being more productive than another for fish.

Methods

Study region

Over the last two decades, the Washington Department of Fish and Wildlife (WDFW) has constructed six side channels in the Skagit River Basin and five on the Olympic Peninsula in the Hoh River and Quillayute River basins (Fig. 1). The mountainous headwaters of these rivers are primarily composed of forested lands managed for park wilderness, recreation, and commercial forestry. Land use in the alluvial lowlands is mixed commercial forestry, hobby farms, and low-density residential housing. The climate is characterized by cool summers and mild winters, with the majority of rain falling between October and June. Forests are dominated by conifers such as Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and sitka spruce (*Picea sitchensis*), with the deciduous species red alder (*Alnus rubra*) and big leaf maple (*Acer macrophyllum*) common at wetter, lower elevations (Franklin and Dyrness 1988). The greatest abundance and diversity of riverine fish occur within the family Salmonidae, including five species of salmon (chum, coho, Chinook (*Oncorhynchus tshawytscha*), pink (*Oncorhynchus gorbuscha*), and sockeye (*Oncorhynchus nerka*)), two species of trout (rainbow (*Oncorhynchus mykiss*) and cutthroat (*Oncorhynchus clarkii*)), two species of char (dolly varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*)), and mountain whitefish (*Prosopium williamsoni*). Other fish present include three species of lamprey (genus *Lampetra*), threespine stickleback (*Gasterosteus aculeatus*), and numerous sculpin of the genus *Cottus* (Wydoski and Whitney 2003).

Study design

We used a posttreatment study design, selecting paired reference channels similar in size and form and in close proximity to each constructed side channel (Table 1). The constructed channels themselves were all based on a similar design: trapezoidal channels excavated over existing groundwater swales and set back from the river channel a minimum of 30 m, with little or no gradient, connected to the mainstem river at their downstream end only, with logs and rootwads cabled in as cover elements, spawning gravel added to the channel bottom, banks planted with red alder, and channel sides armored with large boulders (i.e., rip-rap) for erosion control and to create rock interstices suitable as juvenile fish cover (Fig. 2). Dikes constructed from material excavated during project construction provided flood protection and prevented the river from backwatering into the side channels, except at very high flows. Project age at sampling ranged from 1 to 16 years. Reference channels were more heterogeneous but typically were small side channels fed by both groundwater and surface water, with the upstream mainstem connection active only at high flows. Purely groundwater-fed side channels were not common features in the landscape. At all constructed and reference channels, winter base flows were typically less than 0.3 $m^3 \cdot s^{-1}$ and, with a few exceptions during the late summer, exhibited perennial flow.

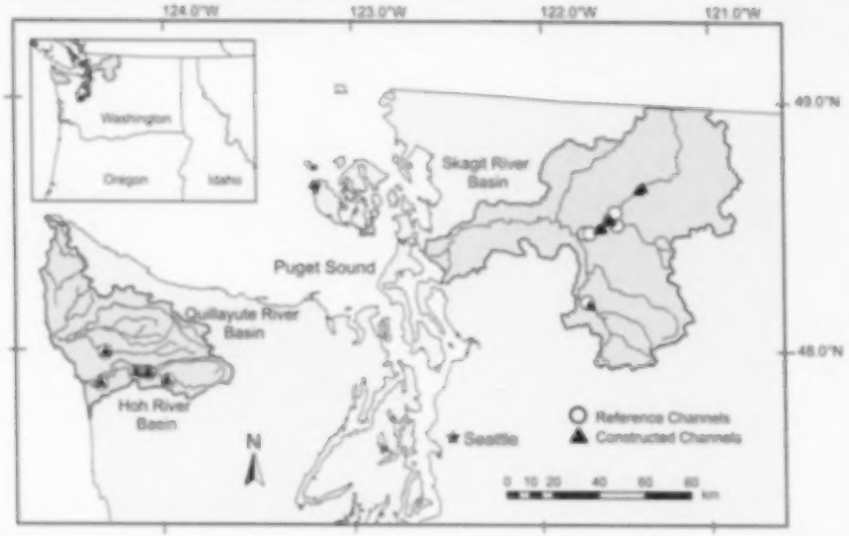
At each of the paired sites, we sampled during two seasons: in the late winter (February–March) before the spring outmigration of salmonid smolts and in the late summer (August–September) before early fall freshets. Skagit River sites were sampled in the winter and summer of 2001, while Olympic Peninsula sites were sampled in the summer of 2002 and winter of 2003. Physical habitat and fish use data were collected during winter and summer at all sites; invertebrate and water chemistry data were collected during summer only; temperature data were collected year-round.

Data collection and analysis

Fish densities were estimated by snorkel surveys. Snorkeling is a relatively noninvasive methodology for working with endangered or threatened species, is well suited to the exceptional visibility typical of our study channels, and allowed us to sample a large number of sample units within a short period of time (Nielsen 1998; Roni and Fayram 2000). Snorkel surveys were conducted during daylight hours in the summer and at least 1 h after sunset in the winter, as juvenile salmonids are typically nocturnal (foraging primarily at night) below 10 °C (Metcalfe et al. 1999; Roni and Fayram 2000). Three individuals served as snorkelers for the duration of the study, with the same two observers snorkeling both the paired treatment and reference channels. Snorkel data were analyzed to determine total fish density and the relative abundance of different species. For purposes of statistical analyses, we combined counts of rainbow and cut-

© 2005 NRC Canada

Fig. 1. Study region, with location of constructed (▲) and reference (○) channels within the three western Washington river basins. Inset map shows location in the Pacific Northwest, USA.



throat trout (hereafter referred to as "trout"), as it is very difficult to distinguish between these two species at lengths less than 100 mm, particularly when snorkeling (Roni and Fayram 2000). As snorkeling does not target benthic fishes such as sculpin and lamprey, we limited our analyses to salmonids. For Skagit River sites, we also conducted summer electrofishing surveys to directly measure fish for size comparisons between constructed and reference channels (Roni and Fayram 2000).

Concurrent with summer snorkel surveys, we collected three invertebrate samples from each study channel. Invertebrates are an important food source for fish and other predators, play a key role in nutrient cycling, and are good indicators of local site conditions in that they are not migratory (Merritt and Cummins 1996). Because riffle habitat was absent from a number of our study channels, we sampled invertebrates from pools using a benthic core (three replicates, 5-cm diameter, 10-cm depth, 500-μm mesh sieve). Invertebrates were counted and identified in the lab to the lowest practical taxonomic level (typically species or genus) to determine mean total abundance and taxa richness. We also calculated the percentage of invertebrates occurring within the aquatic insect orders Ephemeroptera, Plecoptera, and Trichoptera, a grouping referred to as "EPT" that generally includes those invertebrates most sensitive to disturbance (Merritt and Cummins 1996).

We characterized physical habitat at each study site by measuring channel length, gradient, and mean wetted width, by recording depth, substrate type, and presence of in-channel cover along transects perpendicular to flow and by recording habitat types following the definitions of Bisson et al. (1982). We defined in-channel cover as elements potentially providing cover to juvenile fish: wood, aquatic vegetation, undercut banks, boulder crevices, water depth (>1.0 m), and overhanging riparian vegetation. Riparian canopy cover was measured using a point-intercept spherical densiometer. For all wood greater than 10 cm in diameter and 1 m in length, we recorded size class by diameter, total length, and the percentage falling within the active channel. We summarized these data into the following five physical habitat parameters: (1) mean depth (m), (2) percent slow-water habitat (proportion of channel occurring as pools and glides), (3) percent in-channel cover (proportion of channel at which in-channel fish cover present), (4) percent canopy cover (mean canopy closure across the length of the channel), and (5) wood density within the active channel (mean volume of wood divided by channel surface area; $m^3 \cdot m^{-2}$).

Water chemistry and temperature can affect fish both directly via physiological stress and indirectly via influences on primary and secondary productivity (Groot and Margolis 1991; Kiffney et al. 2005). For water chemistry analyses, we collected water column samples from three well-mixed reaches of each study channel, typically a riffle or glide near where invertebrates were collected. Samples were kept frozen for spectrophotometer analysis of dissolved organic carbon (DOC), total (dissolved and suspended organic and inorganic) nitrogen (N) and phosphorous (P), and nitrate (NO_3), nitrite (NO_2), ammonium (NH_4), and phosphate (PO_4). To evaluate temperature, we installed continuously recording temperature loggers at each constructed and reference channel and in the mainstem river between each study pair. Loggers were placed approximately midway up the study channel, suspended slightly above the channel bottom, and set to record temperature at 1-h intervals. We analyzed these data for daily mean, minimum, and maximum temperature over the two seasons prior to snorkel surveys: summer (1 June – 30 September) and winter (1 October – 31 January).

We performed paired *t* tests to evaluate differences between constructed and reference channels in the fish, invertebrate, and physical habitat parameters described above. We compared temperature parameters between constructed, reference, and mainstem sites using two-way analysis of variance (ANOVA), blocking by site. For analyses where we found significant differences, we applied Tukey's multiple

© 2005 NRC Canada

Table 1. Natural features of paired constructed and reference side channels.

Study site	Year constructed	Annual precipitation (cm·year^{-1})	Major lithology (type)	Elevation (m)		River kilometre		Surface area (ha)	
				Constructed	Reference	Constructed	Reference	Constructed	Reference
Skagit River Basin									
Park Slough I	1985	191	Alluvium	137	142	142	126	0.32	0.08
Constant	1991	216	Glacial drift	275	342	148	144	0.27	1.14
Park Slough II	1992	191	Alluvium	138	116	143	127	0.18	0.80
Illabot I	1995	178	Alluvium	81	71	115	110	0.28	0.34
Taylor	1998	178	Alluvium	111	108	124	124	0.67	0.23
Illabot II	2001	178	Alluvium	81	71	115	110	0.47	0.19
Olympic Peninsula									
Mosley	1991	357	Sandstone	206	204	58	58	0.13	0.02
Lewis	1994	406	Sandstone	122	115	46	46	0.27	0.22
Young	1994	330	Sandstone	96	86	39	38	0.48	0.36
Nolan	1996	279	Alluvium	26	25	12	12	0.30	0.07
Raymier	1998	330	Alluvium	75	71	40	39	0.20	0.14

Note: River kilometre is the total distance from the mouth of the study channel to saltwater. Surface area was calculated as total channel length times mean wetted width. Elevation and major lithology at each study channel were derived from 10-m resolution digital elevation models, and geological data were acquired from the United States Geological Survey (USGS). Mean annual precipitation is averaged across United States Department of Agriculture data from 1961 to 1990.

Fig. 2. (*a*) The excavation of a typical constructed side channel and (*b*) a completed side channel with placed wood and planted red alders. Photos were taken at two different side channels on the Skagit River.

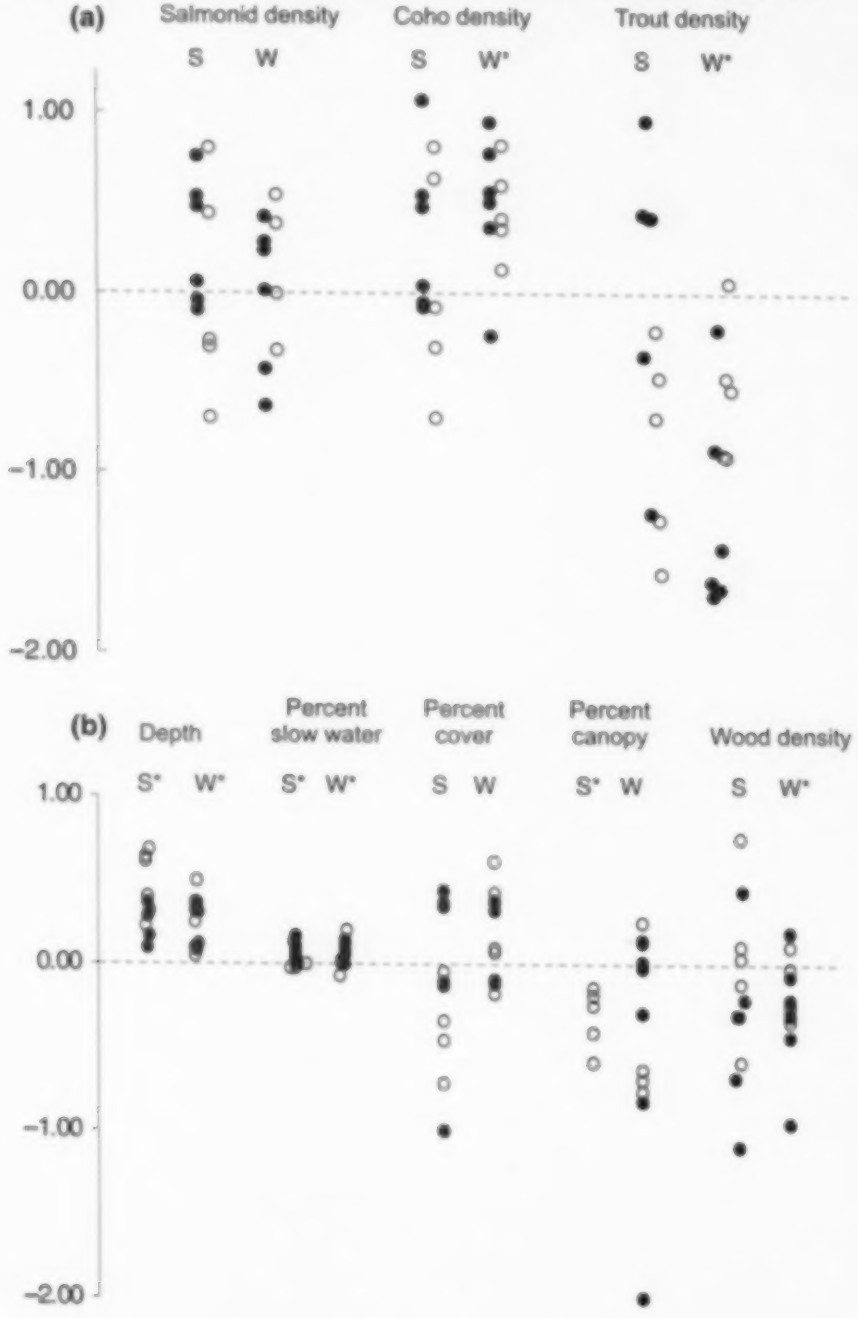
comparison procedure to channel type. Water chemistry was compared across different lithologies using a one-way ANOVA. We used simple linear regression to evaluate the relationship between fish density and selected physical (depth, percent slow water, wood density), chemical (N, P, DOC), biological (total invertebrate abundance and taxa richness), and temperature (daily minimum, mean, and maximum) study parameters, as well as between project age and the log ratio of treatment to reference values for the above parameters. Model residuals were examined for approximate normality, independence, and equality of variance. All statistical analyses were performed using the statistical software program "R" (Ihaka and Gentleman 1996). We used a significance level of $\alpha = 0.05$.

Results

Juvenile coho salmon were the most numerically abundant salmonid at out study side channels, comprising 90% of fish at both channel types during the summer. This proportion remained approximately the same in constructed channels during the winter but decreased to 47% in reference channels.

© 2005 NRC Canada

Fig. 3. Strip plots of the log of the constructed-to-reference ratio (c:r) of mean values for (*a*) fish density and (*b*) physical habitat parameters during summer (S) and winter (W) sampling. Skagit study pairs are indicated by solid circles and Olympic pairs are indicated by open circles. Log(c:r) values = 0, no difference in mean values between channel types; log(c:r) values > 0, constructed greater; log(c:r) values < 0, reference greater. An asterisk (*) indicates that $p < 0.05$ for two-tailed paired t test.



Trout fry were the next most numerically abundant fish observed in both types of channels. Based on snorkel observations of trout greater than 100 mm in length (40% of the total number of trout enumerated throughout the study), the ratio between rainbow and cutthroat trout was approximately equal, with no strong seasonal or regional patterns detected. This observation was supported by electrofish surveys conducted at Skagit River sites, where 42% of captured trout

© 2005 NRC Canada

Table 2. Mean values (±1 SD) for fish density, benthic invertebrate, physical habitat, and water chemistry parameters at constructed and reference study sites for summer (August–September) and winter (February–March).

	Summer		Winter	
Study parameter	Constructed	Reference	Constructed	Reference
Fish density	$n = 11$	$n = 11$	$n = 11$	$n = 11$
Total salmonids (fish·m^{-2})	2.14 (±1.60)	1.29 (±0.89)	0.81 (±0.87)	0.81 (±0.96)
Coho (fish·m^{-2})	2.07 (±1.51)	1.18 (±0.95)	0.77 (±0.87)*	0.21 (±0.20)*
Trout (fish·m^{-2})	0.07 (±0.13)	0.11 (±0.14)	0.04 (±0.04)*	0.60 (±0.94)*
Benthic invertebrates	$n = 10$	$n = 10$	$n = 0$	$n = 0$
Total abundance (no.)	57 (±54)	46 (±32)	NC	NC
Taxa richness (no.)	7.6 (±3.8)	7.6 (±2.9)	NC	NC
EPT taxa (%)	4.7 (±6.4)	3.3 (±4.1)	NC	NC
Physical habitat	$n = 11$	$n = 11$	$n = 11$	$n = 11$
Depth (m)	0.36 (±0.13)*	0.16 (±0.07)*	0.45 (±0.19)*	0.25 (±0.09)*
Slow water (%)	93 (±11)*	83 (±13)*	95 (±7)*	82 (±13) *
In-channel cover (%)	33 (±22)	52 (±30)	36 (±10)	28 (±15)
Canopy (%)	41 (±13)*	81 (±8)*	40 (±34)	70 (±27)
Wood density (m^3·m^{-2})	0.03 (±0.02)	0.06 (±0.05)	0.03 (±0.02)*	0.06 (±0.04)*
Water chemistry	$n = 11$	$n = 10$	$n = 0$	$n = 0$
Dissolved organic carbon (μg·L^{-1})	0.63 (±0.50)	0.72 (±0.50)	NC	NC
Total nitrogen (μg·L^{-1})	206 (±81)	275 (±149)	NC	NC
Total phosphorous (μg·L^{-1})	25 (±8)	35 (±22)	NC	NC
Phosphate (μg·L^{-1})	3.3 (±1.9)	3.5 (±2.9)	NC	NC
Nitrate (μg·L^{-1})	69 (±62)	113 (±106)	NC	NC
Nitrite (μg·L^{-1})	0.46 (±0.56)	0.67 (±0.84)	NC	NC
Ammonium (μg·L^{-1})	7.5 (±6.9)	13.45 (±29)	NC	NC

Note: An asterisk (*) indicates significant differences exist between constructed and reference channels (two-tailed paired t test, $p < 0.05$). NC, data not collected for that season; EPT, Ephemeroptera, Plecoptera, and Trichoptera.

(>100 mm) were rainbow trout and 58% were cutthroat trout. Juvenile Chinook salmon were present in very low densities at approximately half of the study sites, as were char. We did not detect any statistically significant difference in total salmonid density between constructed and reference channels for either the summer or winter (Fig. 3*a*). During the summer, mean salmonid density in constructed channels was 2.1 fish·m^{-2} (compared with 1.3 fish·m^{-2} in reference channels), decreasing to 0.8 fish·m^{-2} in both channel types during the winter (Table 2). Coho density was higher in constructed channels for both seasons, but only significantly so during the winter. Conversely, trout density was higher in reference channels, but again only significantly so during the winter ($p < 0.05$, two-tailed paired t test, $n = 11$; Fig. 3*a*). Based on summer electrofishing conducted at Skagit River sites, we did not detect any significant difference in coho fork length between constructed and reference channels ($p > 0.05$, $n = 6$, two-tailed paired t test).

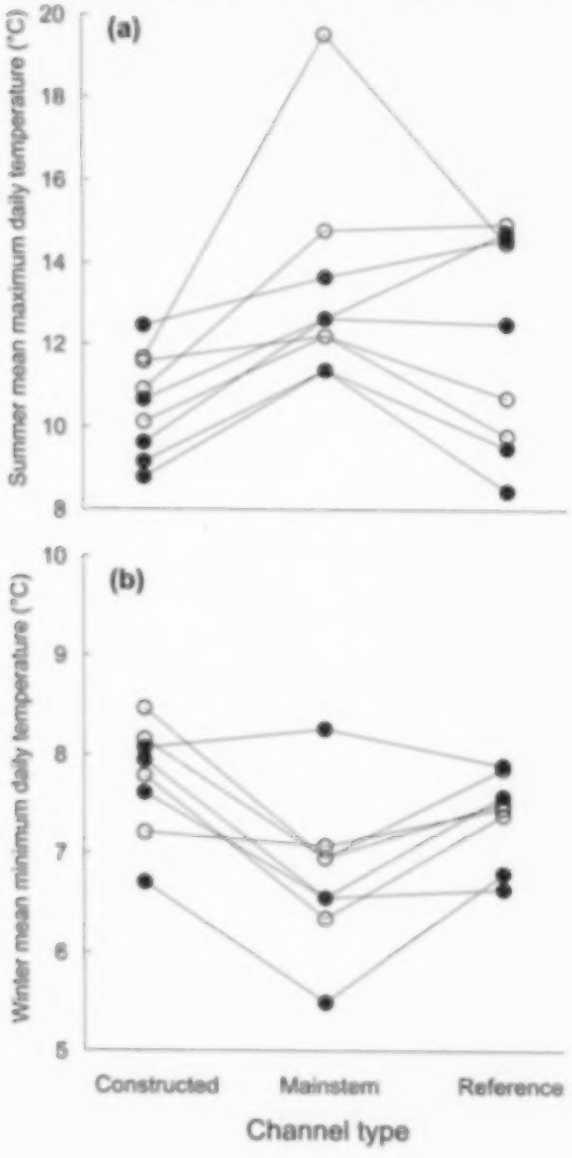
Four of the five physical habitat variables measured were significantly different between constructed and reference channels (depth, percent slow-water habitat, percent canopy coverage, and wood density; Fig. 3*b*). The mean depth of constructed channels was approximately twice that of reference channels for both summer and winter, and over 90% of the linear lengths of constructed channels were composed of slow-water habitat such as pools and glides, a significantly higher proportion than in reference channels (Table 2). Conversely, mean canopy coverage in reference channels was roughly twice that in constructed channels, but only significantly so in the summer (Table 2). Wood density was also higher in reference channels, but these differences were only statistically significant for winter data (Table 2). We did not detect differences in the extent of in-channel fish cover between channel type for either season.

Water chemistry and benthic invertebrate parameters also did not differ significantly between constructed and reference channels. Although mean values for all seven water chemistry parameters tested (DOC, N, P, NO_3, NO_2, NH_4, and PO_4) were greater in reference channels, variability was high within channel types (Table 2). We did not detect any differences in water chemistry parameters relative to major lithology type ($p > 0.05$, ANOVA). Both mean abundance and total taxa richness of benthic invertebrates were very similar between constructed and reference channels (Table 2). The most numerically abundant taxa found in benthic core samples were Chironomids, Oligochaetes, and various crustaceans. Insects from the EPT grouping typically represented less than 5% of the total sample.

Although we did not detect significant differences in mean daily mean temperature (T_{mean}) between channel types, reference channels had significantly higher mean daily maximum temperatures (T_{max}) than constructed channels in the summer and significantly colder mean daily minimum temperatures (T_{min}) in the winter ($p < 0.05$, Tukey's test; Fig. 4). During the summer, mean daily maximum temperature at reference channels was 12.2 °C, compared with 10.6 °C at constructed channels. During the winter, mean daily minimum temperatures at reference channels and constructed channels averaged 7.3 °C and 7.8 °C, respectively. Constructed channels were significantly cooler in the summer and warmer in the

© 2005 NRC Canada

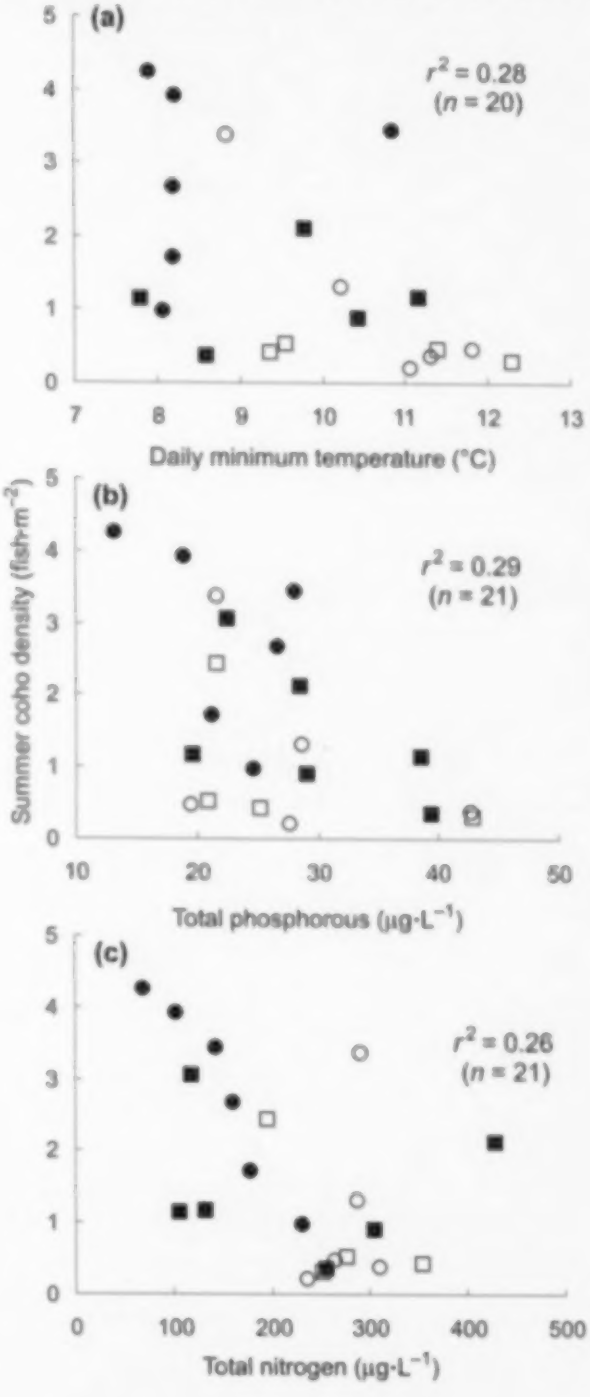
Fig. 4. Seasonal temperatures at grouped constructed, mainstem, and reference channels for (*a*) summer mean maximum daily temperature and (*b*) winter mean minimum daily temperature. Skagit locations are indicated by solid circles and Olympic locations are indicated by open circles. Not all paired constructed and reference channels are plotted with corresponding mainstem data, as a number of loggers were lost during high flows.



winter than the mainstem river ($p < 0.05$, Tukey's test). We did not detect any differences in temperature between the mainstem and reference channels, which had greater surface water connections.

As coho salmon were typically the dominant fish species present at our study sites, we focused our analyses of fish use on both total salmonid density and coho density. We did

Fig. 5. Relationships between mean summer coho (*Oncorhynchus kisutch*) density and (*a*) daily minimum temperature, (*b*) total phosphorous, and (*c*) total nitrogen. Skagit constructed channels are indicated by solid circles and reference channels are indicated by solid squares; Olympic constructed channels are indicated by open circles and reference channels are indicated by open squares.



© 2005 NRC Canada

not detect any significant correlations between fish density (total salmonid or coho) and any of the six study parameters (mean depth, percent slow water, wood density, T_{mean}, T_{min}, and T_{max}) evaluated during the winter. Of the 11 parameters we examined in the summer (same as winter, plus N, P, DOC, and total invertebrate abundance and taxa richness), only T_{max}, N, and P were significantly correlated with coho density (Fig. 5; $p < 0.05$). Although none of these three parameters was correlated with each other, individually none explained more than 30% of the observed variability in summer coho density. With the exception of winter canopy cover ($r^2 = 0.42$, $p < 0.05$, $n = 11$), we did not detect significant relationships between age and any of the physical, chemical, or invertebrate response ratios. For fish, only total summer salmonid density was positively correlated with project age ($r^2 = 0.37$, $p < 0.05$, $n = 11$). In terms of other measured factors that may have contributed to fish density observations, there was no correlation with project size, but there was a weak positive correlation with river kilometre ($r^2 = 0.23$, $p < 0.05$, $n = 22$), reflecting regional differences between Skagit River and Olympic Peninsula channels.

Discussion

The constructed side channels evaluated in this study supported densities of juvenile salmonids equal to or greater than levels observed in natural side channels. Similar to other studies that have evaluated fish use of off-channel habitats (Swales and Levings 1989; Nickelson et al. 1992*a*; Solazzi et al. 2000), juvenile coho salmon were the most numerically abundant species in our study channels. This was particularly true of the constructed channels, where coho typically comprised over 90% of fish present during both the winter and summer sampling periods. The mean coho densities we observed in these 11 western Washington constructed channels (2.1 coho·m^{-2} in summer and 1.2 coho·m^{-2} in winter) are comparable with values reported in similar studies of constructed channels in British Columbia. Working on both groundwater- and surface-water-fed constructed channels in the Fraser River and Squamish River basins, Sheng et al. (1990) and Giannico and Hinch (2003) observed mean smolt production densities of 1–3 coho·m^{-2}, while Decker (1999) reported mean summer coho densities of 3.7 coho·m^{-2}, declining to 0.2 coho·m^{-2} in the winter. The 11 Washington constructed channels also compare favorably with other stream habitats in terms of coho density: Roni and Fayram (2000) seldom observed winter densities above 0.5 coho·m^{-2} in western Washington streams, while Nickelson et al. (1992*b*) reported mean winter densities of 0.2–1.6 coho·m^{-2} and summer densities of 1.0–1.6 coho·m^{-2} in constructed and natural pools in coastal Oregon streams.

Summer coho density appeared to be most influenced by a combination of water temperature and water chemistry. While we did not find any significant correlations for the winter months, fewer measurements were collected during the winter, and temperature records were less complete due to high flows. Project age was not significantly correlated with fish density, although this relationship may have been complicated by the fact that two of the youngest channels were built as spurs onto existing channels (new channels excavated perpendicular to and connected to existing channels), a potentially confounding factor in our study design. Where age likely did play a role was in differences observed in physical habitat between constructed and reference channels.

Constructed channels were more structurally simple than reference channels, particularly the most recently constructed sites. Constructed channels had little or no riffle habitat, lower total wood density, and less canopy coverage. As riparian vegetation planted alongside constructed channels matures, these trees will likely contribute more wood to the active bankfull channel and differences in canopy closure will also likely decrease. As juvenile coho typically exhibit a preference for woody debris (Bustard and Narvar 1975; Bisson et al. 1982; Sandercock 1991), we were surprised that we did not see any correlation between coho density and wood density in our study. In a comparative study of wood placement in two constructed side channels, one fed by surface water and the other by groundwater, Giannico and Hinch (2003) suggest that the benefits of warmer winter temperature in groundwater channels may somewhat override the importance of wood as cover for juvenile coho because of a lower vulnerability to predation.

In comparison to both reference channels and the mainstem river, constructed channels stayed cooler during the summer and warmer during the winter. That these primarily groundwater-fed constructed channels exhibited a less variable temperature regime than the reference channels fed by both groundwater and surface water is not surprising and is in line with previous studies (Sheng et al. 1990; Giannico and Hinch 2003). While both summer and winter temperature at constructed and reference channels were well within the acceptable range for juvenile coho (Sandercock 1991), even small differences in temperature may make some habitats more desirable than others to fish (Giannico and Hinch 2003). In the winter when low temperatures cause juvenile salmonids to become more sluggish (increased response time and decreased swimming speed), even slightly colder temperatures may increase vulnerability to predation by birds and mammals (Metcalfe et al. 1999). During the summer, warmer temperatures result in higher fish metabolic rates and a corresponding increase in food requirements (Welsh et al. 2001).

Given the strong groundwater influence at constructed channels, we also expected that water chemistry might differ from reference channels (Ford and Naiman 1989). However, none of the water chemistry variables we tested was significantly different between channel types. Given our relatively small sample size ($n = 11$) and the high variability observed in nutrient levels both within and between different channels, we may have lacked sufficient statistical power to detect real differences. Our results do concur with findings by Giannico and Hinch (2003), who detected no differences in nutrient concentrations between a surface water fed and groundwater-fed constructed side channel, but differ from those of Decker (1999), who found that phosphorous concentrations were over a magnitude greater in groundwater-fed channels. Overall, the nutrient concentrations observed in both types of channels in our study were comparable to concentrations typical in undeveloped Pacific Northwest streams and, with the amount of canopy closure present at our study sites, likely did not limit primary productivity (Welch et al. 1998; Kiffney et al. 2005).

© 2005 NRC Canada

The lack of observed difference between invertebrate assemblages at constructed and reference channels could in part be due to similarities in nutrient levels or may also be a factor of sample design. Although invertebrate diversity and density are typically highest in riffle habitat (Merritt and Cummins 1996), we sampled invertebrates from pools, as many of the constructed channels contained no riffles. Our mean benthic invertebrate abundance of 52 individuals from benthic core samples was likely too low for an accurate assessment of taxa composition, and we recommend that future studies sample invertebrates over a larger area (either collect more cores or use a device that samples a larger surface area) within these constructed side channels. While a lack of riffle habitat in constructed channels could potentially mean a less diverse input of invertebrates for fish, other food resources such as terrestrial insect inputs and chum fry and carcass remains are also utilized by juvenile coho (Sheng et al. 1990; Bilby et al. 1998).

Although we did not conduct spawning surveys as part of this study, such information would likely have aided in the interpretation of our results on a number of levels. By locating side channels over areas of groundwater upwelling and providing appropriately sized gravels, the constructed channels are intended to provide spawning, as well as rearing, habitat for both coho and chum salmon (Sheng et al. 1990; Bonnell 1991; Cowan 1991). Potentially higher initial seeding of constructed channels may be one reason for observed differences in juvenile coho densities relative to reference channels. However, as coho salmon have been shown to migrate long distances from summer rearing areas to off-channel habitats to overwinter (Peterson 1982*a*), it is also possible that higher coho densities in constructed channels reflect higher mainstem emigration relative to reference channels. As we did not track the movement of fish into and out of our study channels over the course of the study, we cannot distinguish these two sources. Based on smolt trapping conducted previously by the Washington Department of Fish and Wildlife at a number of our study sites, fish movement tends to occur primarily during the first freshets in the fall and in the spring after fry emerge and are seeking out new habitats (D. King, Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501, personal communication). Our sampling windows of late summer and late winter were selected as periods when fish movement was likely relatively low.

Potential indirect effects of variable spawning densities between constructed and reference channels include differences in available food resources and nutrient inputs via carcass decomposition and extent of bioturbation of the channel bed from redd construction (Bilby et al. 1998; Kiffney et al. 2005). While studies from British Columbia indicate that constructed channels may require periodic maintenance to clear spawning gravels of sediment and detritus (but more so in surface water than groundwater channels; Sheng et al. 1990; Lister and Finnigan 1997), none of the channels evaluated in this study has shown an appreciable decrease in depth over time, even at sites constructed over a decade ago (C. Detrick, Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501, personal communication). This could be due in part to frequent disturbance to the channel bed during redd construction by mass spawners such as chum salmon, with further implications for invertebrate production (Minakawa and Gara 2003).

Because of the timing of our sampling, we did not evaluate chum salmon use at our study channels. Constructed side channels in the Skagit River Basin were designed to target chum, as well as coho, and smolt-trapping data indicate that these channels are heavily used by both species (C. Detrick, Washington Department of Fish and Wildlife, 600 Capitol Way N., Olympia, WA 98501, personal communication). While chum fry have a relatively short residency time in fresh water (Groot and Margolis 1991), their presence could influence coho side-channel use via increased availability of food resources (both from chum fry and carcasses; Sheng et al. 1990), as well as via the physical changes to the channel benthos mentioned above.

Recommendations

The constructed groundwater-fed side channels evaluated in this study were successful in creating juvenile salmonid habitat, particularly for coho salmon. Nonetheless, our results suggest some potential improvements in project design. The constructed channels are fairly artificial in appearance and more homogenous than natural side channels in terms of physical habitat diversity and relative abundance of various fish species. Trout were present in very low densities at constructed channels (<0.07 trout·m^{-2}, combined rainbow and cutthroat), with winter densities significantly less than those observed in reference channels (0.60 trout·m^{-2}). Restoration efforts that consider the specific habitat requirements of more than simply one species are likely to have a more positive long-term effect on the larger landscape (Roni et al. 2002; Pess et al. 2005). Although coho may typically be the most abundant fish present, many other species of fish utilize side channels and other off-channel habitats at various life history stages (Lister and Finnigan 1997); these fish are in turn dependent on the invertebrates, amphibians, diatoms, and other stream organisms that make up the aquatic food web. Restoration projects that seek to mimic existing off-channel habitats in all their heterogeneity are most likely to capture this full suite of functions. In deciding how best to direct limited conservation and restoration funds, a watershed assessment should first be performed to help determine if side-channel creation is an appropriate restoration strategy for a given floodplain (Pess et al. 2005). In highly modified landscapes (e.g., urban or agricultural areas) where floodplain complexity has been severely compromised, side-channel construction may be particularly desirable. In less disturbed river basins, similar goals may be better met by protecting or reconnecting existing off-channel habitats, two strategies which are often less costly and less disruptive than construction of new habitat (Roni et al. 2002).

Acknowledgements

We thank B. Barkdul, C. Detrick, D. King, and T. Powell from the Washington State Department of Fish and Wildlife and W. Scarlett from the Washington State Department of Natural Resources for their assistance in site selection and study design. The National Park Service, National Forest Service, Washington State Department of Natural Resources, Rayonier Timber Company, and Green Crow Timber gra-

© 2005 NRC Canada

ciously allowed us access to their lands; A. Pratt, B. Sodeman, F. Sommers, and D. Werner provided support in the field; J. Ayers, S. Baker, and R. Holland assisted with data analysis and figure preparation; and M. Liermann provided statistical consultation. Invertebrate samples were processed by Rhithron Biological Associates, and water chemistry samples were analyzed by the University of Washington's School of Oceanography. We thank G. Pess, M. Liermann, and two anonymous reviewers for their thoughtful comments on earlier drafts of this manuscript. Funding for this study was provided by a grant from the Northwest Fisheries Science Center, NOAA.

References

Beechie, T., Beamer, E., and Wasserman, L. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. N. Am. J. Fish. Manag. **14**: 797–811.

Bilby, R.E., Fransen, B.R., Bisson, P.A., and Walter, J.K. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Can. J. Fish. Aquat. Sci. **55**: 1909–1918.

Bisson, P.A., Nielsen, J.L., Palmason, R.A., and Grove, L.E. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low stream flows. *In* Acquisition and utilization of aquatic habitat inventory information. *Edited by* N.B. Armantrout. American Fisheries Society, Bethesda, Md. pp. 62–73.

Bonnell, R.G. 1991. Construction, operation, and evaluation of groundwater-fed side channels for chum salmon in British Columbia. Am. Fish. Soc. Symp. **10**: 109–124.

Bustard, D.R., and Narver, D.W. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. **32**: 667–680.

Cowan, L. 1991. Physical characteristics and intragravel survival of chum salmon in developed and natural groundwater channels in Washington. Am. Fish. Soc. Symp. **10**: 125–131.

Decker, A.S. 1999. Effects of primary production and other factors on the size and abundance of juvenile coho salmon in artificial off-channel habitat. M.Sc. thesis, University of British Columbia, Vancouver, B.C.

Ford, T.E., and Naiman, R.J. 1989. Groundwater – surface water relationships in boreal forest watersheds: dissolved organic carbon and inorganic nutrient dynamics. Can. J. Fish. Aquat. Sci. **46**: 41–49.

Franklin, J.F., and Dyrness, C.T. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oreg.

Giannico, G.R., and Hinch, S.G. 2003. The effect of wood and temperature on juvenile coho salmon winter movement, growth, density and survival in side channels. River Res. Appl. **19**: 219–231.

Groot, C., and Margolis, L. (*Editors*). 1991. Pacific salmon life histories. UBC Press, Vancouver, B.C.

Ihaka, R., and Gentleman, R. 1996. R: a language for data analysis and graphics. J. Comput. Graph. Statist. **5**: 299–314.

Kiffney, P.M., Bilby, R.E., and Sanderson, B.L. 2005. Monitoring the effects of nutrient enrichment on freshwater ecosystems. *In* Methods for monitoring stream and watershed restoration. *Edited by* P. Roni. American Fisheries Society, Bethesda, Md. pp. 237–264.

Lister, D.B., and Finnigan, R.J. 1997. Rehabilitating off-channel habitat. Fish habitat rehabilitation procedures. *In* Watershed restoration technical circular No. 9. *Edited by* P.A. Slaney and D.O. Zaldokas. Watershed Restoration Program, Ministry of Environment, Lands and Parks, Vancouver, B.C. pp. 7.1–7.29.

Lister, D.B., Marshall, D.E., and Hickey, D.G. 1980. Chum salmon survival and production at seven improved groundwater-fed spawning areas. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 1595.

Merritt, R.W., and Cummins, K.W. (*Editors*). 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Metcalfe, N.B., Fraser, N.H.C., and Burns, M.D. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. J. Anim. Ecol. **68**: 371–381.

Minakawa, N., and Gara, R.I. 2003. Effects of chum salmon redd excavation on benthic communities in a stream in the Pacific Northwest. Trans. Am. Fish. Soc. **132**: 598–604.

National Marine Fisheries Service (NMFS). 2003. Updated status of federally listed ESUs of west coast salmon and steelhead. Report by the West Coast Salmon Biological Review Team, Northwest Fisheries Science Center, Seattle, Wash. (http://www.nwfsc.noaa.gov/).

Nickelson, T.E., Rodgers, J.D., Johnson, S.L., and Solazzi, M.F. 1992*a*. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhyncus kisutch*) in Oregon coastal streams. Can. J. Fish. Aquat. Sci. **49**: 783–789.

Nickelson, T.E., Solazzi, M.F., Johnson, S.L., and Rodgers, J.D. 1992*b*. Effectiveness of selected stream improvement techniques to create suitable summer and winter rearing habitat for juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Can. J. Fish. Aquat. Sci. **49**: 790–794.

Nielsen, J.L. 1998. Scientific sampling effects: electrofishing California's endangered fish populations. Fisheries, **23**: 6–12.

Pess, G.R., Morley, S.A., Hall, J.L., and Timm, R.K. 2005. Monitoring floodplain restoration. *In* Methods for monitoring stream and watershed restoration. *Edited by* P. Roni. American Fisheries Society, Bethesda, Md. pp. 127–166.

Peterson, N.P. 1982*a*. Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds. Can. J. Fish. Aquat. Sci. **39**: 1308–1310.

Peterson, N.P. 1982*b*. Population characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) overwintering in riverine ponds. Can. J. Fish. Aquat. Sci. **39**: 1303–1307.

Roni, P., and Fayram, A. 2000. Estimating winter salmonid abundances in small western Washington streams: a comparison of three techniques. N. Am. J. Fish. Manag. **20**: 683–692.

Roni, P., Beechie, T.J., Bilby, R.E., Leonetti, F.E., Pollock, M.M., and Pess, G.P. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. N. Am. J. Fish. Manag. **22**: 1–20.

Sandercock, F.K. 1991. Life history of coho salmon. *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. UBC Press, Vancouver, B.C. pp. 395–445.

Sheng, M.D., Foy, M., and Fedorenka, A.Y. 1990. Coho salmon enhancement in British Columbia using improved groundwater-fed side channels. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 2071.

Solazzi, M.F., Nickelson, T.E., Johnson, S.L., and Rodgers, J.D. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Can. J. Fish. Aquat. Sci. **57**: 906–914.

Swales, S., and Levings, C.D. 1989. Role of off-channel ponds in the life cycle of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Coldwater River, British Columbia. Can. J. Fish. Aquat. Sci. **46**: 232–242.

© 2005 NRC Canada

Tschaplinski, P.J., and Hartman, G.F. 1983. Winter distribution of juvenile coho salmon (*Oncorhyncus kisutsch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Can. J. Fish. Aquat. Sci. **40**: 452–461.

Washington State Department of Fish and Wildlife (WDFW). 1999–2003. Regional Fisheries Enhancement Program Annual Reports. Washington Department of Fish and Wildlife, Olympia, Wash. (http://wdfw.wa.gov/).

Welch, E.B., Jacoby, J.M., and May, C.W. 1998. Stream quality. *In* River ecology and management: lessons from the Pacific coastal ecoregion. *Edited by* R.J. Naiman and R.E. Bilby. Springer, New York. pp. 69–94.

Welsh, H.H., Jr., Hodgson, G.R., Havey, B.C., and Roche, M.F. 2001. Distribution of juvenile coho salmon in relation to water temperatures in tributaries of the Mattole River, California. N. Am. J. Fish. Manag. **21**: 464–470.

Wydoski, R.S., and Whitney, R.R. 2003. Inland fishes of Washington. American Fisheries Society, Bethesda, Md.

© 2005 NRC Canada

Spatial and temporal variance of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea

John K. Horne and Paul D. Walline

Abstract: Mobile acoustic surveys attempt to map and count aquatic organisms without biasing abundance estimates. Horizontal and vertical movements by target species may influence density measurements and net samples during acoustic surveys. To investigate the influence of fish movement on density data, we compared temporal and spatial variability of walleye pollock (*Theragra chalcogramma*) in three sets (2 night, 1 day) of 14.8-km transects in the eastern Bering Sea. Walleye pollock density distributions were also compared with those in the five nearest daytime survey transects. We found that horizontal density distributions did not change at temporal scales ≤4 h and that spatial variance remained consistent at scales ≤2.5 km. Spatial variance density patterns were similar in transects sampled during the day compared with those sampled at night and were also similar in along-shore compared with cross-shore transects. Transects that contained two biological scattering layers could be vertically separated into zooplankton and fish. Spatial variance patterns in the upper zooplankton layer mimicked those of passive tracers, while patterns in the lower layer were consistent with those previously observed for mobile nekton. Current sampling resolution of acoustic surveys adequately captures horizontal spatial variance of walleye pollock in the Bering Sea.

Résumé : Les inventaires acoustiques mobiles cherchent à cartographier et à dénombrer les organismes aquatiques sans fausser les estimations d'abondance. Les déplacements horizontaux et verticaux des espèces ciblées peuvent affecter les mesures de densité et fausser les échantillons nets durant l'inventaire. Afin d'évaluer l'influence des déplacements des poissons sur les données de densité, nous avons comparé la variation temporelle et spatiale chez des goberges de l'Alaska (*Theragra chalcogramma*) dans trois séries (2 de nuit et 1 de jour) de transects de 14,8 km dans l'est de la mer de Béring. Nous avons aussi comparé les répartitions de densité des goberges de l'Alaska à celles obtenues sur les cinq transects d'inventaires de jour les plus proches. Les répartitions horizontales de densité ne changent pas aux échelles temporelles de ≤4 h et la variance spatiale reste uniforme aux échelles de ≤2,5 km. Les patrons de variance de la densité spatiale sont semblables sur les transects inventoriés le jour et la nuit, de même que chez ceux faits parallèlement et perpendiculairement à la rive. Dans les transects qui contiennent deux couches de diffusion biologique, nous pouvons distinguer verticalement le zooplancton et les poissons. Les patrons de variance spatiale de la couche supérieure de zooplancton imitent ceux de traceurs passifs, alors que les patrons de la couche inférieure concordent avec ceux observés antérieurement chez le necton mobile. La résolution actuelle de l'échantillonnage des inventaires acoustiques permet de capter de façon adéquate la variance spatiale horizontale de la goberge de l'Alaska dans la mer de Béring.

[Traduit par la Rédaction]

Introduction

Characterizing the temporal and spatial behaviour of a target species is crucial to the successful census of aquatic nekton (Aglen 1994; Fréon and Misund 1999). Any movement by organisms during assessment surveys potentially biases density and subsequent abundance or biomass estimates. Remote sensing is one approach used to reduce bias by increasing the proportion of the area or volume sampled and by increasing synopticity of a survey. Animal distribution patterns observed using remote sensors such as echosounders are dependent on the aperture of the sensor, the speed of the platform, the sampling rate of the instrument, the grouping of samples, and by organism movements relative to the sensor track. In aquatic surveys, vessel-mounted sensors with small apertures have a limited number of sur-

Received 29 October 2004. Accepted 29 June 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 8 November 2005.
J18381

John K. Horne.[1] University of Washington, School of Aquatic and Fishery Sciences, Box 35520, Seattle, WA 98355, USA, and National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA.
Paul D. Walline. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA.

[1]Corresponding author (e-mail: jhorne@u.washington.edu).

 doi: 10.1139/F05-192 © 2005 NRC Canada

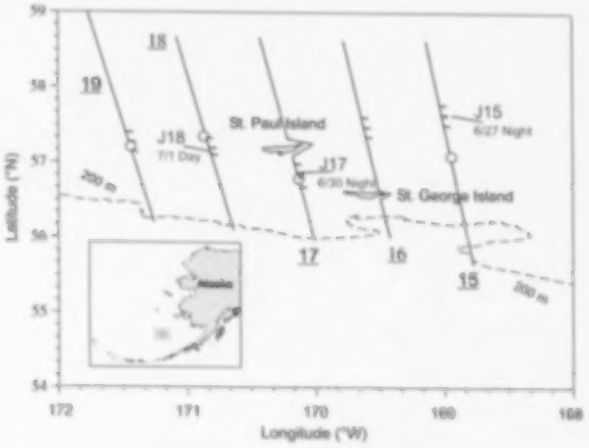
vey design variables that can be controlled by the user: temporal collection of data, spatial resolution of individual and grouped samples, and the spatial pattern of sampling.

A sampling spatial pattern, or survey design, is optimal if samples accurately characterize the abundance and distribution of a population while minimizing sampling effort. Since patchy distributions are a long-recognized trait of pelagic organisms (Hensen 1911; Hardy 1955; Steele 1976), survey designs must be sensitive to the spatial and temporal dynamics of the population being surveyed (Reid et al. 2000). Studies examining effects of dynamic fish distributions on accuracy of numeric or biomass estimates have traditionally focused on estimating uncertainty (e.g., Petitgas 2001; Gimona and Fernandes 2003) or bias of abundance estimates utilizing alternate sample layouts relative to population distributions (e.g., Simmonds and Fryer 1996; Kalikhman and Ostrovsky 1997). Less effort has focused on the effect of individual and aggregation movements relative to sampling resolution and on the potential confounding of animal movements with elapsed sampling time on abundance estimates. The challenge of designing an effective survey is further compounded when the geographic area of interest is large, the sampling speed is slow, and the sampling resolution of survey transects is coarse given the time constraints of a research vessel schedule.

Assessing adult biomass of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea includes all of these challenges. Walleye pollock represents approximately 70% of the groundfish biomass in the eastern Bering Sea (Springer 1992). Commercial fishers took over six million metric tons a year in the late 1980s, but the catch has dropped to around three million metric tons in recent years (source: Food and Agriculture Organization of the United Nations (FAO) Fisheries Global Information System, http://www.fao.org/fi/figis/index.jsp). The highest catches represent up to 5% of the world's fish catch (Bailey et al. 1999). Walleye pollock are found throughout the middle and outer shelf domains of the eastern Bering Sea (Coachman 1986), necessitating a 300 000 km^2 survey area that extends from the Aleutian Island archipelago to the Russian–US border (e.g., Honkalehto et al. 2002). Acoustic surveys have assessed population numbers, biomass, and mapped summer distributions of walleye pollock on the continental shelf and slope at least every 3 years since 1979 (Traynor and Nelson 1985; Wespestad 1993; Karp and Walters 1994). The survey is conducted over 2 months and typically logs a cruise track greater than 18 500 km (i.e., ~10 000 nautical miles, nmi). Since 1991, the cruise track has followed a boustrophedon sampling pattern, where regularly spaced, parallel transects are surveyed in alternating directions along a north–south axis.

Despite the ecological and commercial importance of commercial fish populations, such as walleye pollock, variability in density distributions at the sampling resolution of an acoustic survey (i.e., minimum 0.1-km horizontal integration bins and 10-km transect spacing) is not well described (Brodeur and Wilson 1996; Bailey et al. 1999). We were curious how observed distribution patterns may be confounded by the acoustic sampling resolution or by movement of fish during sampling. Walleye pollock were chosen as a representative species whose distributions and behaviors are typical of semidemersal and pelagic gadoids. A collection of repeated, extracted, and regular acoustic survey transects were used to quantify changes in walleye pollock density as a function of spatial scale and temporal sampling resolution.

Fig. 1. Location of midwater trawls (circles), full acoustic transects (numbers 15 through 19), extracted transects (tic marks on full transects), and repeated acoustic transects (J15, J17, and J18). The rectangle in the inset shows the location of the study transects within the Bering Sea.



Materials and methods

Data collection

An echo integration-trawl survey targeting walleye pollock was conducted on the eastern Bering Sea shelf between 7 June and 2 August 2000 aboard the National Oceanic and Atmospheric Administration (NOAA) ship *Miller Freeman* (see Honkalehto et al. 2002 for survey details). The survey consisted of 29 parallel transects spaced at 37 km (i.e., 20 nmi) and oriented north–south across the continental shelf (Fig. 1). Transect directions in the shelf survey are oriented approximately orthogonal to bathymetric contours and coincide with groundfish survey transects conducted by the same institution.

All regular transects were surveyed during daylight hours (~0500–2400 local time). On 27 June, 30 June, and 1 July, additional sets of 14.8 km (i.e., 8 nmi) transects, repeated four times, were surveyed orthogonal to the regular transects (i.e., east–west along shelf) (Table 1). Each of these short transects took approximately 1 h to complete. Two of the three repeated transect sets (J15 and J17) were conducted during dark hours, while the set on 1 July (J18) was completed during the day. All repeated transects were completed before sunrise or sunset to avoid vertical distribution changes associated with crepuscular periods. The location of repeated transects was determined using a combination of cruise logistics and presence of fish. Throughout the survey, fish were sampled using an Aleutian Wing Trawl (midwater) and an 83/112 eastern bottom trawl to identify species within aggregations or layers and to provide length frequency samples.

© 2005 NRC Canada

Table 1. Walleye pollock (*Theragra chalcogramma*) repeated transect data summary sampled in the eastern Bering Sea during June and July 2000.

Transect	Day (D) vs. Night (N)	Start time	End time
J15a	N	0.3784722	0.41157407
J15b	N	0.4174769	0.45105324
J15c	N	0.4557986	0.48898148
J15d	N	0.4961921	0.53009259
J17a	N	0.3645949	0.39821759
J17b	N	0.4067477	0.44010417
J17c	N	0.4464699	0.47982639
J17d	N	0.4867361	0.52018519
J18a	D	0.1095602	0.14280093
J18b	D	0.1481481	0.18157407
J18c	D	0.1969213	0.23034722
J18d	D	0.2343056	0.26875000

Note: All times are Coordinated Universal Time (UTC). To convert to decimal hours, multiply UTC by 24.

Walleye pollock density was measured using a calibrated Simrad EK 500 splitbeam echosounder (Horten, Norway) operating at 38 kHz (Bodholt et al. 1989). All densities were recorded as nautical area scattering coefficients (s_A, $m^2 \cdot nmi^{-1}$). Acoustic data samples were filtered using an S_v threshold of −70 (dB re 1 m^{-1}), inspected and corrected for bottom integration, vertically integrated from 14 m below the surface to 0.5 m above bottom, and binned at a horizontal distance of 185.2 m (i.e., 0.1 nmi). Since each of the repeated transects was 14.8 km in length, each transect data set contained 80 bins. To examine the potential presence of anisotropic density distributions, two additional 14.8-km sections of transect were extracted from the adjacent north–south survey transects and were binned in the same way. To increase the number of transects examined and to extend the range of the spatial variance analysis, the closest five full survey transects (transects 15–19) were also binned at 185.2-m resolution. Data from the full transects were vertically integrated from 14 m below the surface to 0.5 m or 1.0 m from the bottom (depending on bottom roughness and fish density). All echograms were scrutinized for species, and the analysis of fish was limited to walleye pollock. When plankton formed a layer near the surface, the top of the echo integration layer was lowered to 30 m below the surface. No mixing occurred between walleye pollock and the plankton layer during diel migrations.

Spatial analyses

Scale-dependent spatial variance of walleye pollock density distributions was characterized using spectral analysis (Jenkins and Watts 1968; Koopmans 1974; Chatfield 1984). The density data (i.e., s_A values) were first standardized by subtracting the mean and dividing by the standard deviation, a fast Fourier transform was applied to each set of s_A values, the results squared, and the periodogram smoothed using a triangular filter (Chatfield 1984). Least squares regression lines were fitted to log–log plots of spectral density and frequency. When a change in slope (i.e., an inflection point) was observed, the data were divided in two sections, and separate regression lines were fit to each section. Spectral density values from replicate transects were averaged to facilitate comparison among sets at larger temporal scales.

Three additional metrics were used to examine similarity in the spatial scale-dependence of walleye pollock density distributions. One-dimensional variograms (using s_A values) were constructed for each transect, and then a model was fit by eye using EVA 2 software (Petitgas and LaFont 1997). The presence and characteristics of a nugget, sill, and range were described for each variogram model. Semivariance was also plotted as a function of distance between pairs of points (i.e., lag distance) in each transect. Lag units ranged from twice the horizontal resolution of the data (370 m) to half the distance of a repeated transect (7.4 km). In full transects, lag units started at 10 km. Correlograms were plotted for each transect, and autocorrelation radii were tabulated when the autocorrelation function approached zero (i.e., 0.003 or less).

Temporal analyses

To quantify temporal variability in one-dimensional, walleye pollock densities during 4-h sampling periods, changes in acoustic backscatter at each horizontal sampling bin (45 s) were tabulated as a function of time lag among bins within and among transect repetitions. A set of repeated transects consisted of four passes. There were a total of six possible pairs of time lags for each bin where a difference in density (Δs_A) and a difference in time (Δt) could be calculated. When Δs_A is plotted as a function of Δt, trends in density changes will be seen as deviations from $\Delta s_A = 0$.

Temporal changes in two-dimensional walleye pollock distributions were examined by comparing normalized density distributions between transect pairs within the 14.8-km repeated transect sets. Fish density similarity was investigated at the resolution of an acoustic cell (185 m horizontal by 5 m vertical) and summarized for each transect. The metric used is Syrjala's (1996) analog to a Cramér – von Mises test that compares the sum of squared differences between two cumulative distribution functions. Since the comparison metric is sensitive to the starting cell within a transect, the comparison was calculated starting at each corner of the transect. The final test statistic was an average of the four comparison values (Zimmerman 1993). The level of significance ($\alpha = 0.05$) of the test statistic was determined using a randomization test (Edgington 1980). Cells at corresponding locations in the two transects being compared were randomly assigned to one of the two transects. Densities were then tabulated in cumulative distribution functions for computation of the test statistic. One thousand randomizations were used to compute the empirical distribution function of the test statistic in each comparison. See Syrjala (1996) for additional details.

Results

Fish caught in midwater trawls closest to the repeated transect locations consisted of 35- to 55-cm walleye pollock (see trawl locations in Fig. 1). Some juvenile walleye pollock were caught in the midwater trawl on transect 15. Walleye pollock were vertically dispersed during the two nighttime, repeated-transect series (J15 and J17) and formed a layer between 50- and 75-m depth during the daytime se-

© 2005 NRC Canada

Table 2. Characteristics of walleye pollock (*Theragra chalcogramma*) spatial distribution in repeated, extracted, and regular acoustic transects surveyed in the eastern Bering Sea during summer 2000.

				Variogram		
Series	Transect	s_A ($m^2 \cdot nmi^{-1}$)	Autocorrelation radius (km)	Nugget	Sill	Range (km)
Repeated	J15a	351	—	Yes	No	Slight increase
	J15b	198	0.4	Yes	No	Slight linear increase
	J15c	278	3.3	Yes	No	Linear increase
	J15d	221	2.8	Yes	No	Nonlinear increase
	J17a	216	2.4	Yes	Yes	6.5
	J17b	198	0.2	Yes	No	Slight linear increase
	J17c	191	0.4	Yes	No	Pure nugget
	J17d	212	0.6	Yes	Small	Almost pure nugget
	J18a	1042	2.2	Yes	Small	~1.8, mostly nugget
	J18b	947	5.6	Yes	No	Irregular increase
	J18c	863	1.7	Yes	No	Slight linear increase
	J18d	1002	2.4	Yes	No	Linear increase
Average		466	2.5			
Extracted	15a	271	0.6	Yes	No	Pure nugget
	15b	297	4.6	Yes	No	Nonlinear increase
	16a	2305	4.6	Small	No	Steep linear increase
	16b	1289	3.9	No	No	Steep linear increase
	17a	923	3.9	Yes	Yes	4.4
	17b	327	1.7	Yes	Yes	~1.8
	18a	1280	2.8	Yes	No	Linear increase
	18b	796	2.2	Yes	Yes	~3.0
	19a	291	3.9	Yes	No	Linear increase
	19b	334	2.2	Yes	Yes	<3.6
Average		658	2.8			
Full	15	344	10.4	Yes	Yes	~37 (9.3)
	16	1548	47.0	Yes	Yes	81.5 (11.1)
	17	3025	53.3	Small	Yes	~88.9 (linear increase)
	18	920	70.7	Yes	Yes	>55.6 (6.5)
	19	907	79.8	Yes	Yes	>185.2 (linear increase)
Average		1349	52.2			

Note: s_A denotes integrated water column acoustic backscatter (1 nmi = 1.852 km). Autocorrelation radius is the distance where the autocorrelation function reaches 0.003 or less. Experimental variograms are described using the presence or absence of a nugget and sill and a characterization of the range. For variograms without a sill, a description of the change in semivariance with lag distance is given. The information in parentheses (for the full transects) describes the model variogram fitted by eye when the maximum lag distance is restricted to the length of the repeated transects (14.8 km).

ries (J18). Near surface zooplankton layers were present during the J17 and J18 series. The upper 30 m of the water column was excluded from the analysis of fish spatial variance for all transects.

Fish densities were consistent within and among repeated transects (Table 2) but lower on average than those observed in the same area during the regular survey tracks (see extracted s_A values). Full survey transects had higher average s_A values than the repeated transects but also contained large sections with no fish. Repeated transects used in this analysis were not made in areas with high densities of walleye pollock.

Dominant spatial scales indicated by peaks in spectral density plots were difficult to visualize within histograms of acoustic fish density (Fig. 2; see also fig. 7.4 in Chatfield 1984). Spectral density values generally decreased from large to small scales, with fluctuating values at higher frequencies in all repeated transects. The peaks and troughs within spectral density plots at higher frequencies did not exactly coincide among repeated transects (Fig. 3). Overall slopes of repeated transects were less than those observed at large scales (i.e., Steep in Table 3). Average transition scales (i.e., inflection points on the spectral density curves), interpreted as aggregation sizes of walleye pollock, were similar among the three repeated transect sets (J15: 2.4 km; J17: 2.8 km; J18: 2.3 km). Averaging spectral density values among repeated transects from each series resulted in smoothed average plots, but fluctuations remained at the higher frequencies (Fig. 3*d*). Average spectral density plots can be characterized by variable maximum values at the largest scale measured (14.8 km for the repeated transects), a continuous negative slope to a scale of approximately 1 km, and a reduced slope at scales less than 1 km.

Within regular survey transects, spectral density plots for walleye pollock differed from those for smaller targets assumed to be zooplankton (Fig. 4). Variance in zooplankton distributions exceeded those of walleye pollock at the largest scales measured. Zooplankton spectral densities decreased at

© 2005 NRC Canada

Fig. 2. Plot of walleye pollock (*Theragra chalcogramma*) density (s_A, $m^2 \cdot nmi^{-1}$) with distance along transect J18d (*a*) and resulting spectral density plot (*b*).

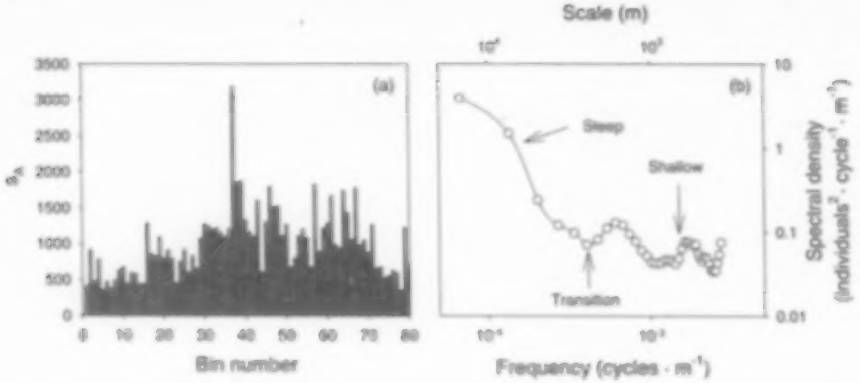
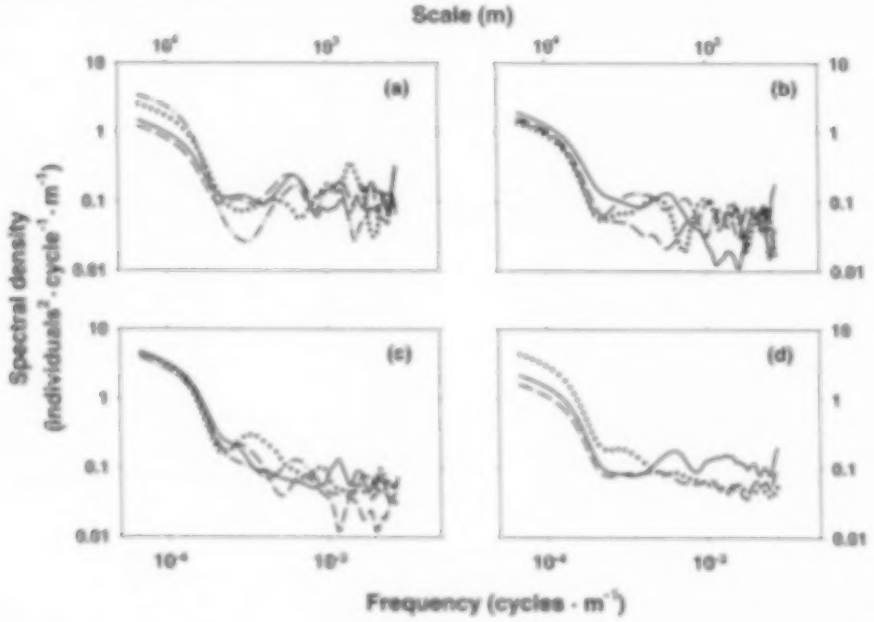


Fig. 3. Spectral density plots for repeated transect night series J15 (*a*) and J17 (*b*), repeated transect day series J18 (*c*), and the average of each series (*d*). For each series, the first repetition was drawn with a solid line, the second with a dashed line, the third with a dotted line, and the fourth with a dash-dotted line.



a relatively uniform rate over the entire range of scales examined. In contrast, walleye pollock spectral densities decreased at the largest scales and were nearly constant at scales ranging from a few kilometers to the minimum scale examined.

The averaged spectral density plot for series J18 was compared with the average spectral density plot from two 8 nmi sections of the adjacent transect 18. This comparison was used to examine the potential for anisotropic walleye pollock distributions during daylight hours. Differences in amplitudes and slopes of the spectral density plots from the north–south (18) and east–west transect series (J18) were slight (Fig. 5). No discernable trends were evident in the two plots, suggesting that observed patterns in fish distributions are not influenced by acoustic transect orientation.

Variograms computed for the repeated transects showed no change or continuous increases in semivariance over the distance examined (7.4 km). Where no sill was evident, models fit to the data resulted in extrapolated ranges of tens to hundreds of kilometers. Variograms for the J15 transect series exhibited a temporal trend (Fig. 6). The variogram of transect J15a did not contain a sill and had a constant semivariance for lag distances of up to 7.4 km. The semivariance of transect J15b linearly increased from the smallest lag distance to a lag distance of 7.4 km. The semivariance of J15c and J15d increased linearly over the sampled range. Patterns

© 2005 NRC Canada

Table 3. Summary of spectral density plot slopes and transition scales for all transects.

Series	Transect	Overall	Steep	Shallow	Transition scale (km)
Repeated	15a	–0.3	–1.7	0.1	2.1
	15b	–0.3	–1.7	–0.25	2.5
	15c	–0.4	–2.4	0	2.5
	15d	–0.6	–3.3	–0.35	2.5
	17a	–0.9	–1.9	–0.4	2.1
	17b	–0.4	–2.1	0.3	1.6
	17c	–0.6	–2.6	–0.3	3.7
	17d	–0.5	–2.6	–0.2	3.7
	18a	–0.8	–2.5	–0.1	2.5
	18b	–1.2	–1.8	0.3	0.9
	18c	–1	–2.7	–0.8	3.7
	18d	–0.9	–2.4	–0.4	2.1
Extracted	15a	–0.6	–2.2	–0.4	3.7
	15b	–0.8	–2	–0.6	3
	16a	–1.8	–1.8	–1.8	0
	16b	–1.8	–1.8	–1.8	0
	17a	–1.3	–1.3	–1.3	0
	17b	–1	–1	–1	0
	18a	–0.4	–1.9	0	3
	18b	–0.9	–2.3	–0.1	1.8
	19a	–0.7	–2.7	0.1	3
	19b	–0.8	–0.8	–0.8	0
Full	15	–0.4	–0.4	–0.4	0
	16	–1.3	–1.3	–1.3	0
	17	–1.2	–1.3	5	0.5
	18	–0.6	–1	0	0.8
	19	–0.8	–0.8	1.4	0.5

Note: Overall slope uses all points in the series, steep is the slope of the section prior to the transition, and shallow is the slope after the transition scale.

Fig. 4. Spectral density plot of the zooplankton layer (all s_A between 14 and 30 m) and that of walleye pollock (*Theragra chalcogramma*) (s_A deeper than 30 m) on transect 18.

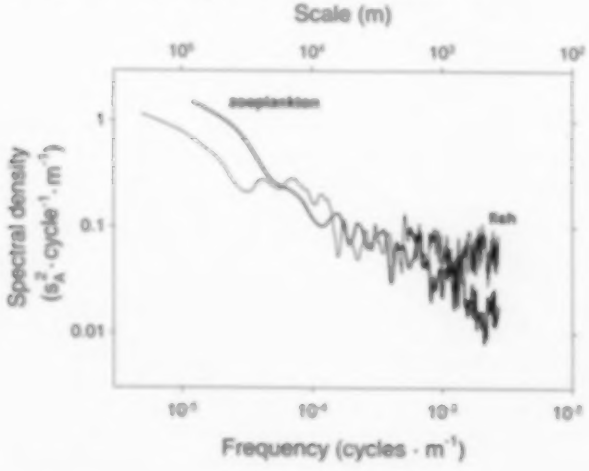


Fig. 5. Averaged spectral density plots from the short transect series J18 (solid line) and two extracted 8-nmi (1 nmi = 1.852 km) orthogonal daytime sections from transect 18 (dashed line).

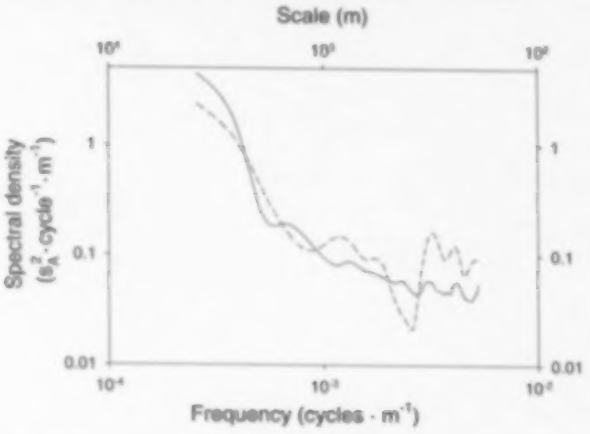
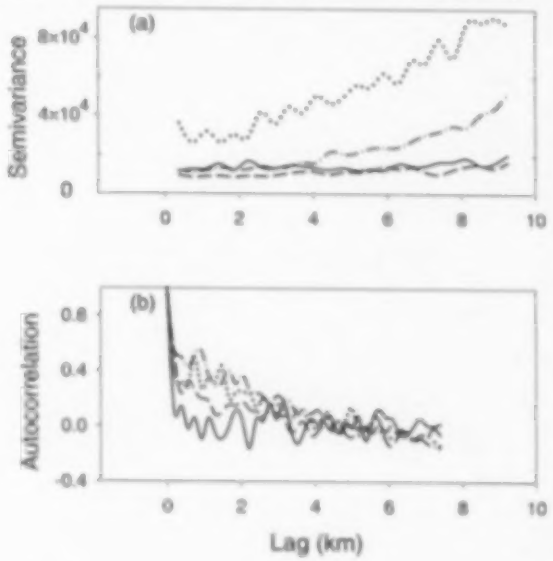


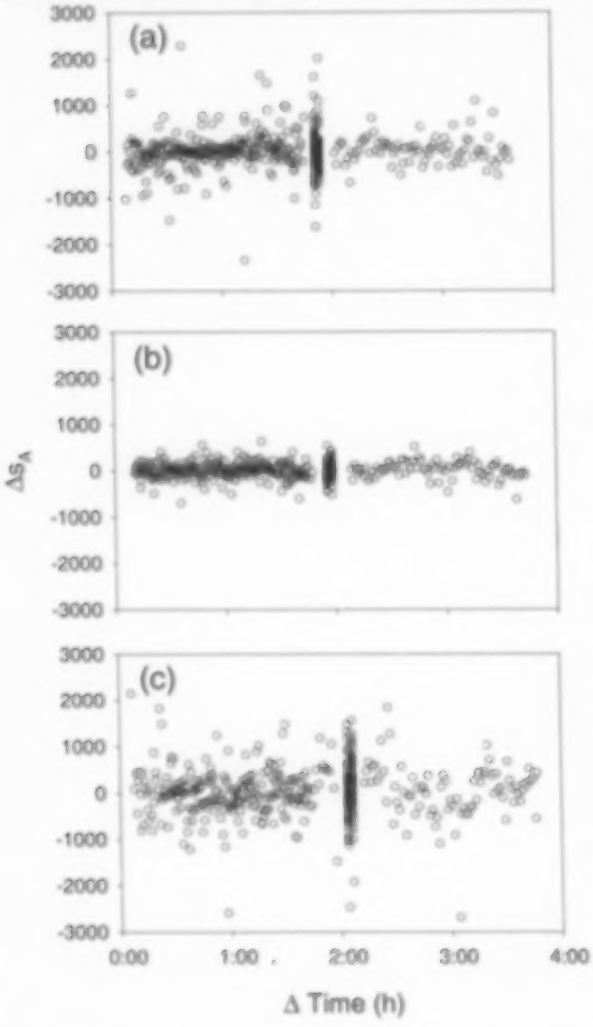
Fig. 6. Variograms (*a*) and correlograms (*b*) of transects J15a (solid), J15b (dashed), J15c (dotted), and J15d (dash-dotted).



observed in variograms of the extracted transects were consistent with those obtained from variography of full transects. In full transects surrounding the repeated transect sampling sites (i.e., transects 15 to 19), all but transect 18 had 56–93 km (i.e., 30–50 nmi) ranges despite poor behaviour in some experimental variograms. The variogram of transect 15 did not follow this trend. Transect 15 was characterized by a large nugget and erratic fluctuations of semivariance with lag distance. When the maximum lag distance in full transects was constrained to match the length of the repeated transects (i.e., 14.8 km), ranges in modeled variograms from full and repeated transects were directly comparable (see values in parentheses, Table 2). All constrained ranges in full

© 2005 NRC Canada

Fig. 7. Change in fish density (Δs_A) plotted as a function of lag time for each repeated transect series J15 (*a*), J17 (*b*), and J18 (*c*).



transects were larger than those observed in repeated transects.

As expected, results from autocorrelation analyses were comparable with those from one-dimensional variography. For all 14.8-km repeated and the extracted sections of complete transects, autocorrelation radii ranged from 0.1 to 5.6 km (Table 2). Autocorrelation radii for the set of complete transects averaged 52.2 km, an order of magnitude larger than the average of the repeated (2.5 km) or extracted (2.8 km) transects. When variograms exhibited nearly pure nugget behavior (e.g., J15a and J17b), the corresponding autocorrelation radii were short (Fig. 6).

Differences in walleye pollock integrated acoustic densities (i.e., s_A values) did not depend on the time difference between samples (Fig. 7). On average, s_A values remained constant at each location (i.e., 185-m horizontal bin) and did not increase as the time interval between any two samples increased. With the exception of five extreme values in the J15 and J18 series, changes in acoustic densities were clustered close to zero for all sample time intervals.

Table 4. Comparison of walleye pollock (*Theragra chalcogramma*) density distributions (s_A, $m^2 \cdot nmi^{-1}$) within repeated 14.8-km (i.e., 8-nmi) transect sets using a modified Cramér – von Mises statistic (cf. Syrjala 1996).

Transect	a	b	c
15a	—	—	—
15b	0.0024 (0.601)	—	—
15c	0.0075 (0.098)	0.0031 (0.552)	—
15d	**0.0269 (0.001)**	**0.0172 (0.018)**	0.0088 (0.091)
17a	—	—	—
17b	0.0107 (0.087)	—	—
17c	0.0108 (0.081)	**0.0232 (0.004)**	
17d	0.0100 (0.089)	0.0080 (0.151)	0.0107 (0.078)
18a	—	—	—
18b	**0.0075 (0.014)**	—	—
18c	**0.0139 (0.001)**	0.0056 (0.055)	—
18d	**0.0201 (0.001)**	0.0057 (0.108)	0.002 (0.486)

Note: *p* values are added in parentheses. Significant differences are in boldface.

Temporal similarity of two-dimensional walleye pollock density distributions differed among and within repeated transect sets (Table 4). Transect 15d differed from 15a and 15b in the first set. Transect 17b was different from 17c in the second set of repeated transects. In contrast, density distributions in transect 18a differed from all other repeated transects in the third transect set. A lower proportion of transects differed in transects sampled during dark hours (3/12) than those that were sampled during daylight hours (3/6) but only one day transect (18a) differed from the other three sampled during the day. No discernable trend was present in two-dimensional density differences between transect pairs as a function of time lag between or among repeated samples. The Cramér – von Mises test does not facilitate comparison among repeated transect sets.

Discussion

Techniques used to quantify variability in walleye pollock density distributions are applicable to many semidemersal or pelagic fish species and can be used in the design of mobile nekton acoustic sampling (Table 5). Spectral density curves from regular and repeated transect sets all contained slight negative slopes at small spatial scales. Observed near-constant variance at scales less than ~2 km means that horizontal bin sizes at or less than 2 km will include variability in walleye pollock density distributions. In contrast, the presence of steep and shallow slopes within spectral density plots of zooplankton layers from regular survey transects suggests that analytic cell sizes for mixed nektonic communities should be 200 m or less to characterize variation in zooplankton density distributions. The presence of steep and shallow slopes in spectral density plots of repeated and regular transects indicates that densities of walleye pollock aggregations were consistent at spatial scales equal to or less than ~2.5 km. The implication for survey sampling is that aggregation or school sizes are ~2.5 km in chord distance and that midwater or bottom trawl sampling used to verify

© 2005 NRC Canada

Table 5. Summary of analytic patterns observed, biological interpretation, and implication for acoustic abundance surveys.

Transect analytic pattern	Biological interpretation	Survey implication
Regular and repeated: slight negative slope at small scales	Constant small-scale variance	Scrutinizing resolution ≤1 nmi is fine
Regular: two layers with different spectral slopes		
Upper steeper than lower	Zooplankton, passive-like	To characterize zooplankton density distribution, must scrutinize ≤200 m
Lower small scale flatter	Fish, mobile	To characterize fish density distribution, must scrutinize ≤1 nmi
Repeated: two parts steep and shallow	Consistent density distributions at scales ≤2.5 km (patch size)	Patch size diameter ~2.5 km or 32 min at 2.5 knots for trawl sample
Alongshore vs. crosshore: break at same scale on both spectra; similar slopes on pairs of segments	Isotropic density distributions	Transect direction does not matter (should be checked for each species and season)
Day vs. night repeated: similar slopes and amplitudes within spectra	Density distributions are similar day and night	Sampling can be same day and night (should be checked for each species and season)
Temporal dependence: zero change in s_A as a function of time	No change in fish density distributions at temporal scales ≤4 h	Can return to spot for net sample within 4 h
Two-dimensional repeated: no consistent change with elapsed time	Fish density changing over small temporal scales	Difficult to catch specific fish
	Density changes horizontally and vertically	Should fish shortly after observation if want to sample a particular layer

Note: 1 nmi = 1.852 km.

species composition and to collect length frequency data must not exceed 32 min at a trawling speed of 1.3 $m \cdot s^{-1}$ (i.e., 2.5 knots) to remain within an observed aggregation. The similarity in spectral density plots from along-shore and cross-shore transects suggests isotropic density distributions of walleye pollock, and assuming that these samples are representative, the direction of transect sampling or trawling does not matter. Similarities in spectral density plots between day and night transects imply that variability in vertically integrated density distributions during summer months does not have a strong diel component and that transect layout and sampling can remain constant throughout a 24-hour period. If a significant portion of the target species occurs within the near-bottom dead zone, then biased density estimates may result. This observation is based on integrated water column backscatter using a limited number of samples and may not be consistent in other seasons, in depth-stratified samples, or for other fish species. Since changes in integrated water column fish densities were not dependent on elapsed time between acoustic measurements, changes in fish densities occurred at temporal scales ≤4 h. Therefore, representative species identification and length frequency samples can be obtained from a trawl sample as long as a location is fished within 4 h of the corresponding acoustic sample. It may be difficult to catch a specific school when trawling, but the net contents should be representative of individuals within an aggregation.

A variety of metrics can be used to characterize aggregation or patch sizes. The range parameter of a variogram is interpreted as the biological patch size (Rossi et al. 1992). The same interpretation is used for the autocorrelation radius (Legendre and Fortin 1989; Kalikhman and Ostrovsky 1997) and for slope changes in spectral density plots (Horne and Schneider 1997). In this study, estimates of walleye pollock aggregation sizes differed depending on the metric used and, in part, on the length of the original transect. Extrapolated ranges from variogram models of full transects ranged between 37 and 185 km, autocorrelation radii were 2–3 km in length, and patch size inferred from changes in spectral density slopes averaged ~2.5 km. Inferred patch sizes were similar between autocorrelation radii and changes in spectral density slopes. Variogram ranges from full transects or calculated using restricted lag distances exceeded ranges of all other transects. Since the nugget contains measurement error and spatial variance at scales smaller than the lag unit, ranges smaller than the lag unit will not be detected. Increased lag distances used in calculating variograms for full transects are believed to contribute to the mismatch between ranges at small and large scales. Slopes of zooplankton and walleye pollock spectral density plots indicate that scale-dependent density distributions differed between the two groups. The shape and slope of the zooplankton spectral density plot is consistent with those of krill in the Southern Ocean (Weber et al. 1986; Levin et al. 1989), which mimic scale-dependent, spatial distribution patterns of passive tracers. The shallower slope of the walleye pollock spectral density plot is attributed to movement associated with aggregative behaviours (see also Horne and Schneider 1997).

The analytic techniques used in this study do have limitations. All three surface pattern techniques (Legendre and Fortin 1989) are based on estimates of lagged covariance functions: spectral analysis (Platt and Denman 1975), autocorrelation radii (Legendre and Fortin 1989), and variography (Rossi et al. 1992; Petitgas 1993). Lagged covariance techniques are sensitive to the presence of zero counts that may overestimate covariances (Fasham 1978; Legendre and Fortin 1989; Horne and Schneider 1997) and also sensitive to extreme values that may bias results (O'Driscoll et al.

© 2005 NRC Canada

2000). In our study, overall densities in repeated transects were low, but only 2 of 1760 cells within the 14.8-km transects contained zero s_A values. Wavelet analysis, an alternative to spectral analysis and variograms (Bradshaw and Spies 1992), can be used to investigate both local and global scale-dependent patterns but is typically used with nonstationary series (Hudgins et al. 1993; Lau and Weng 1995). The global wavelet spectrum has been shown to be equivalent to the true power spectrum (Percival 1995). We standardized all density series used in this study to ensure stationarity and focused the analysis on the global binning and timing of acoustic samples.

Temporal variability in walleye pollock densities differed depending on the observation scale and the number of dimensions used in the analysis. At temporal scales of 4 h or less and horizontal spatial scales of 185 m, acoustic backscatter values differed between some transect pairs in two spatial dimensions but not among cells when backscatter was integrated through the water column. This pattern was consistent within and among repeated transect sets, whether the sampling occurred during light or dark hours. The relation between sample unit size and spatial aggregation pattern has been shown to influence spatial variability (Sawyer 1989; Yamamura 1990) but additional effects due to flux (i.e., spatial movement over time) have received less attention (Gaston and McArdle 1994). A relevant resource management issue is the maintenance of population densities despite ongoing reductions in population abundances (cf. McArdle and Gaston 1993; Rose and Kulka 1999; O'Driscoll et al. 2000). Conflation of spatial with temporal variability has also been shown to systematically overestimate temporal variance in population abundance estimates (Stewart-Oaten et al. 1995).

Acoustic-based density measurements were not adversely affected by spatiotemporal movements of walleye pollock during summer months. Based on our samples, walleye pollock distributions appear to be isotropic, at least at spatial scales ranging from 185 m to 7.4 km (i.e., 0.1 to 4 nmi). The resulting acoustic density measurements and trawl samples were not dependent on the direction of sampling. Obviously, a single examination for the presence of anisotropy over a relatively short range of spatial and temporal scales is not definitive. Large-scale distributions should be detectable using the 37-km (i.e., 20-nmi) transect spacing currently used in Bering Sea surveys. Additional knowledge on the net flux of the population over the summer months, the degree of anisotropy over an increased scale range, and the association with strong depth or environmental gradients is required to eliminate potential sources of bias in walleye pollock abundance estimates. Empirical data collections on fish fluxes combined with computer simulations of alternate survey designs are recommended as the next step in this line of research.

Acknowledgements

We thank Dr. E. Loggerwell, Dr. S. Syrjala, Dr. R. O'Driscoll, and Mr. N. Williamson for reviews that clarified the manuscript. This study was supported by the Alaska Fisheries Science Center (NA17RJ1232-AM01) and the Office of Naval Research (N0014-00-1-0180).

References

Aglen, A. 1994. Sources of error in acoustic estimation of fish abundance. *In* Marine fish behaviour in capture and abundance estimation. *Edited by* A. Fernö and S. Olsen. Fishing News Books, London. pp. 107–133.

Bailey, K.M., Quinn, T.J., II, Bentzen, P., and Grant, W.S. 1999. Population structure and dynamics of walleye pollock, *Theragra chalcogramma*. Adv. Mar. Biol. **37**: 179–255.

Bodholt, H., Nes, H., and Solli, H. 1989. A new echo sounder system. Proc. Instit. Acoust. **11**: 123–130.

Bradshaw, G.A., and Spies, T.A. 1992. Characterizing canopy gap structure in forests using wavelet analysis. J. Ecol. **80**: 205–215.

Brodeur, R.D., and Wilson, M.T. 1996. Mesoscale acoustic patterns of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can. J. Fish. Aquat. Sci. **53**: 1951–1963.

Chatfield, C. 1984. The analysis of time series: an introduction. Fourth edition. Chapman and Hall, London.

Coachman, L.K. 1986. Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. Cont. Shelf Res. **5**: 23–28.

Edgington, E.S. 1980. Randomization tests. Second edition. Marcel Dekker, New York.

Fasham, M.J. 1978. The application of some stochastic processes to the study of plankton patchiness. *In* Spatial pattern in plankton communities. *Edited by* J.H. Steele. Plenum Press, New York. pp. 131–156.

Fréon, P., and Misund, O.A. 1999. Dynamics of pelagic fish distribution and behaviour. Fishing New Books, Oxford, UK.

Gaston, K.J., and McArdle, B.H. 1994. Temporal variability of animal abundances. Philos. Trans. R. Soc. Lond. B Biol. Sci. **345**: 335–358.

Gimona, A., and Fernandes, P.G. 2003. A conditional simulation of acoustic survey data: advantages and potential pitfalls. Aquat. Living Resour. **16**: 123–129.

Hardy, A.C. 1955. A further example of the patchiness of plankton distribution. Deep Sea Res. (Pap. Mar. Biol. Oceanogr.) **3**(Suppl.): 7–11.

Hensen, V. 1911. Das leben im ozean nach zahlungen seiner Bewohner. Übersicht und resultaten der quantitativen untersuchungen. Ergebn. Plankton Expdn. derHumboldt Stiftung V.

Honkalehto, T., Williamson, N., Hanson, D., McKelvey, D., and de Blois, S. 2002. Results of the echo integration-trawl survey of walleye pollock (*Theragra chalcogramma*) conducted in the southeastern Bering Sea shelf and slope in June and July 2002. NOAA Fisheries, Alaska Fisheries Science Center, Seattle, Wash. AFSC Processed Rep.

Horne, J.K., and Schneider, D.C. 1997. Spatial variance of mobile aquatic organisms: capelin and cod in Newfoundland coastal waters. Philos. Trans. R. Soc. Lond. B Biol. Sci. **352**: 633–642.

Hudgins, L., Friehe, C.A., and Mayer, M.E. 1993. Wavelet transforms and atmospheric turbulence. Phys. Rev. Lett. **71**: 3279–3282.

Jenkins, G.M., and Watts, D.G. 1968. Spectral analysis and its applications. Holden-Day, San Francisco.

Kalikhman I., and Ostrovsky, I. 1997. Patchy distribution fields: survey design and adequacy of reconstruction. ICES J. Mar. Sci. **54**: 809–818.

Karp, W.A., and Walters, G.E. 1994. Survey assessment of semipelagic gadoids: the example of walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea. Mar. Fish. Rev. **56**: 8–22.

Koopmans, L.H. 1974. The spectral analysis of time series. Academic Press, New York.

Lau, L.-M., and Weng, H. 1995. Climate signal detection using wavelet transform: how to make a time series sing. Bull. Am. Meteorol. Soc. **76**: 2391–2402.

© 2005 NRC Canada

Legendre, P., and Fortin, M.J. 1989. Spatial pattern and ecological analysis. Vegetatio, **80**: 107–138.

Levin, S.A., Morin, A., and Powell, T.M. 1989. Patterns and processes in the distribution and dynamics of Antarctic krill. Scientific Committee for the Conservation of Antarctic Marine Living Resources (SC-CAMLR)-VII/BG/20. pp. 281–296.

McArdle, B.H., and Gaston, K.J. 1993.The temporal variability of populations. Oikos, **67**: 187–191.

O'Driscoll, R.L., Schneider, D.C., Rose, G.A., and Lilly, G.R. 2000. Potential contact statistics for measuring scale-dependent spatial pattern and association: an example of northern cod (*Gadus morhua*) and capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. **57**: 1355–1368.

Percival, D.P. 1995. On estimation of the wavelet variance. Biometrika, **82**: 619–677.

Petitgas, P. 1993. Geostatistics for fish stock assessments: a review and an acoustic application. ICES J. Mar. Sci. **50**: 285–298.

Petitgas, P. 2001. Geostatistics in fisheries survey design and stock assessment: models, variances and applications. Fish Fish. **2**: 231–249.

Petitgas, P., and Lafont.,T. 1997. Eva2: estimation of variance version 2. A geostatistical package on Windows 95 for estimating precision of fish stock assessment surveys. ICES CM 1997/Y 22.

Platt, T., and Denman, K.L. 1975. Spectral analysis in ecology. Annu. Rev. Ecol. Syst. **6**: 189–210.

Reid, D., Scalabrin, C., Petitgas, P., Masse, J., Aukland, R., Carrera, P., and Georgakarakos, S. 2000. Standard protocols for the analysis of school based data from echo sounder surveys. Fish. Res. **47**: 125–136.

Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Can. J. Fish. Aquat. Sci. **56**(Suppl. 1): 118–127.

Rossi, R.E., Mulla, D.J., Journel, A.G., and Franz, E.H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monogr. **62**: 277–314.

Sawyer, A.J. 1989. Inconstancy of Taylor's b: simulated sampling with different quadrat sizes and spatial distributions. Res. Popul. Ecol. **31**: 11–24.

Simmonds, E.J., and Fryer, R.J. 1996. Which are better, random or systematic acoustic surveys? A simulation using North Sea herring as an example. ICES J. Mar. Sci. **53**: 39–50.

Springer, A. 1992. A review: walleye pollock in the North Pacific — how much difference do they really make? Fish. Oceanogr. **1**: 80–96.

Steele, J.H. 1976. Patchiness. *In*. The ecology of the seas. *Edited by* D.H. Cushing and J.J. Walsh. Blackwell Scientific Publications, London. pp. 98–115.

Stewart-Oaten, A., Murdoch, W.W., and Walde, S.J. 1995. Estimation of temporal variability in populations. Am. Nat. **146**: 519–535.

Syrjala, S.E. 1996. A statistical test for a difference between the spatial distributions of two populations. Ecology, **77**: 75–80.

Traynor, J.J., and Nelson, M.O. 1985. Results of the U.S. hydroacoustic survey of pollock on the continental shelf and slope. Int. North Pac. Fish. Comm. Gull. **44**: 192–199.

Weber, L.H., El-Sayed, S.Z., and Hampton, I. 1986. The variance spectra of phytoplankton, krill and water temperature in the Antarctic Ocean south of Africa. Deep-Sea Res. **33**: 1327–1343.

Wespestad, V.G. 1993. The status of Bering Sea pollock and the effect of the "Donut Hole" fishery. Fisheries, **18**: 18–24.

Yamamura, K. 1990. Sampling scale dependence of Taylor's power law. Oikos, **59**: 121–125.

Zimmerman, D.L. 1993. A bivariate Cramér-von Mises type of test for spatial randomness. Appl. Stat. **42**: 43–54.

© 2005 NRC Canada

Can otolith elemental signatures record the capture site of Patagonian toothfish (*Dissostichus eleginoides*), a fully marine fish in the Southern Ocean?

J.R. Ashford, C.M. Jones, E. Hofmann, I. Everson, C. Moreno, G. Duhamel, and R. Williams

Abstract: Otolith chemistry has been successfully used to reconstruct the environmental history experienced by estuarine-dependent teleost fish, including movement between estuaries and coastal areas. However, application has been more limited in species exposed exclusively to oceanic waters, where gradients in physical and chemical properties are less extreme. To test whether otolith elemental signatures record spatial information in an oceanic species, we sampled otoliths from Patagonian toothfish (*Dissostichus eleginoides*) and used an inductively coupled plasma mass spectrometer (ICP-MS) coupled to a laser ablation system to target the outer otolith edges corresponding to the period immediately before capture. Using multivariate analysis of variance and multivariate discriminant analysis, we found that edge signatures discriminated toothfish by geographic region with near complete success: only 5% of fish caught off South America and in the Antarctic were misclassified to sampling areas in the other region. Moreover, edge signatures showed strong differences between sampling areas within each region: fish captured off South America classified to sampling areas therein with 79%–84% success, and Antarctic fish classified to sampling areas therein with 50%–67% success. These results compare favourably with rates of classification for estuarine-dependent fish, demonstrating that otolith elemental signatures can discriminate the geographic provenance of oceanic and estuarine-dependent fish.

Résumé : La chimie des otolithes permet de retracer avec succès le passé environnemental des poissons téléostéens qui dépendent des estuaires et, en particulier, leurs déplacements entre les estuaires et les milieux côtiers. La méthode est cependant plus rarement utilisée chez les espèces qui sont exposées exclusivement aux eaux de l'océan, car les gradients des propriétés physiques et chimiques y sont moins marqués. Afin de vérifier si les signatures des éléments dans les otolithes enregistrent des renseignements de nature spatiale chez une espèce océanique, nous avons prélevé des otolithes de la légine australe (*Dissostichus eleginoides*) et nous avons utilisé un spectromètre de masse à plasma inductif (ICP-MS) couplé à un système d'ablation laser pour cibler les couches externes des otolithes qui correspondent à la période qui précède immédiatement la capture. Une analyse de variance multidimensionnelle et une analyse discriminante multidimensionnelle démontrent que les signatures sur les couches externes permettent de discriminer les otolithes d'après la région géographique avec un succès presque complet; seuls 5 % des poissons capturés au large de l'Amérique du Sud et dans l'Antarctique sont mal classifiés dans des zones d'échantillonnage de l'autre région. De plus, les signatures des couches externes indiquent de fortes différences entre les zones d'échantillonnage de chacune des régions : les poissons récoltés au large de l'Amérique du Sud sont placés à 79–84 % dans des zones d'échantillonnage de la région et ceux de l'Antarctique à 50–67 % dans des zones d'échantillonnage de cette région. Ces résultats se comparent avantageusement aux taux de classification obtenus chez les poissons associés aux estuaires, ce qui démontre que les signatures des éléments dans les otolithes permettent de reconnaître l'origine géographique des poissons océaniques aussi bien que celle des poissons estuariens.

[Traduit par la Rédaction]

Received 11 October 2004. Accepted 27 May 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 9 November 2005.
J18349

J.R. Ashford[1] and C.M. Jones. Center for Quantitative Fisheries Ecology, Old Dominion University, Norfolk, VA 23529, USA.
E. Hofmann. Center for Coastal Physical Oceanography, Old Dominion University, Norfolk, VA 23529, USA.
I. Everson. Environmental Sciences Research Centre, School of Applied Sciences, Anglia Polytechnic University, East Road, Cambridge, UK.
C. Moreno. Instituto de Ecología y Evolución, Universidad Austral de Chile, Valdivia, Chile.
G. Duhamel. Museum National d'Histoire Naturelle, 43 Rue Cuvier, 75231 Paris CEDEX 05, France.
R. Williams. Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia.

[1]Corresponding author (e-mail: jashford@odu.edu).

 doi: 10.1139/F05-191 © 2005 NRC Canada

Introduction

Recent advances in ecology have highlighted the importance of spatial considerations in population dynamics. For instance, critical habitats may contribute disproportionately to recruitment (Beck et al. 2003), and linkage between geographic areas through migration can fundamentally affect population dynamics (e.g., Pulliam 1988; Polacheck 1990; Hanski and Simberloff 1997). Where mortality exceeds recruitment, changes in immigration and emigration may determine local persistence or extinction.

To measure fish movement and link spawning adults to earlier habitat, researchers have historically used genetic markers and artificial tags. However, genetic markers cannot link fish to geographic area specifically, but rather to a population, limiting their use for identifying the critical habitats used by fish that survive to reproduce. Moreover, genetic techniques rely on identifying unique fixed markers when populations are known to be separate, usually during spawning. On the other hand, artificial tags can only link fish to the area where they were marked or recaptured, and the technique depends on several assumptions that can be difficult to meet. Moreover, tagging the number of fish necessary to generate sufficient recaptures is costly and logistically challenging.

In the last decade, however, new technology has led to renewed interest in trace and minor element analysis of otoliths. Because they have similar properties, divalent elements substitute for Ca in the aragonite lattice of the otolith. Consistent concentrations of Sr, Ba, and Mn recorded for fishes between the ambient water, blood plasma, and otolith suggest that seawater concentrations influence the rate at which the elements are incorporated into the otolith (Campana 1999). Moreover, validating studies have estimated this relationship experimentally by manipulating ambient Sr/Ca and Ba/Ca and measuring their resulting otolith concentrations (Bath et al. 2000). The preferred instrumentation available to make these measurements is inductively coupled plasma mass spectrometry (ICP-MS) because of its sensitivity and mass resolution (Campana 1999). When coupled with lasers, ICP-MS combines these advantages with the capacity to sample material at fine spatial scales (Jones and Chen 2003).

As a result, researchers have successfully used natural elemental markers in otolith growth increments to reconstruct the environmental history experienced by estuarine-dependent fish, including movement between oceanic and estuarine environments (see Thresher (1999) for review). However, application of laser ICP-MS to exclusively marine species has been more limited because of the perception that otolith chemistry is less effective as a natural marker for discriminating between environments offshore, where gradients in physical and chemical properties are much less pronounced. Yet earlier studies discriminated between fish from different capture areas (Thresher 1999), even when they used dissolved whole otoliths, which integrated the otolith chemistry over the entire life history prior to capture (Edmonds et al. 1989, 1991). Furthermore, the environment was sufficiently heterogeneous between five spawning grounds for elemental markers deposited in otolith nuclei to discriminate between Atlantic cod (*Gadus morhua*) returning as adults (Campana et al. 1994).

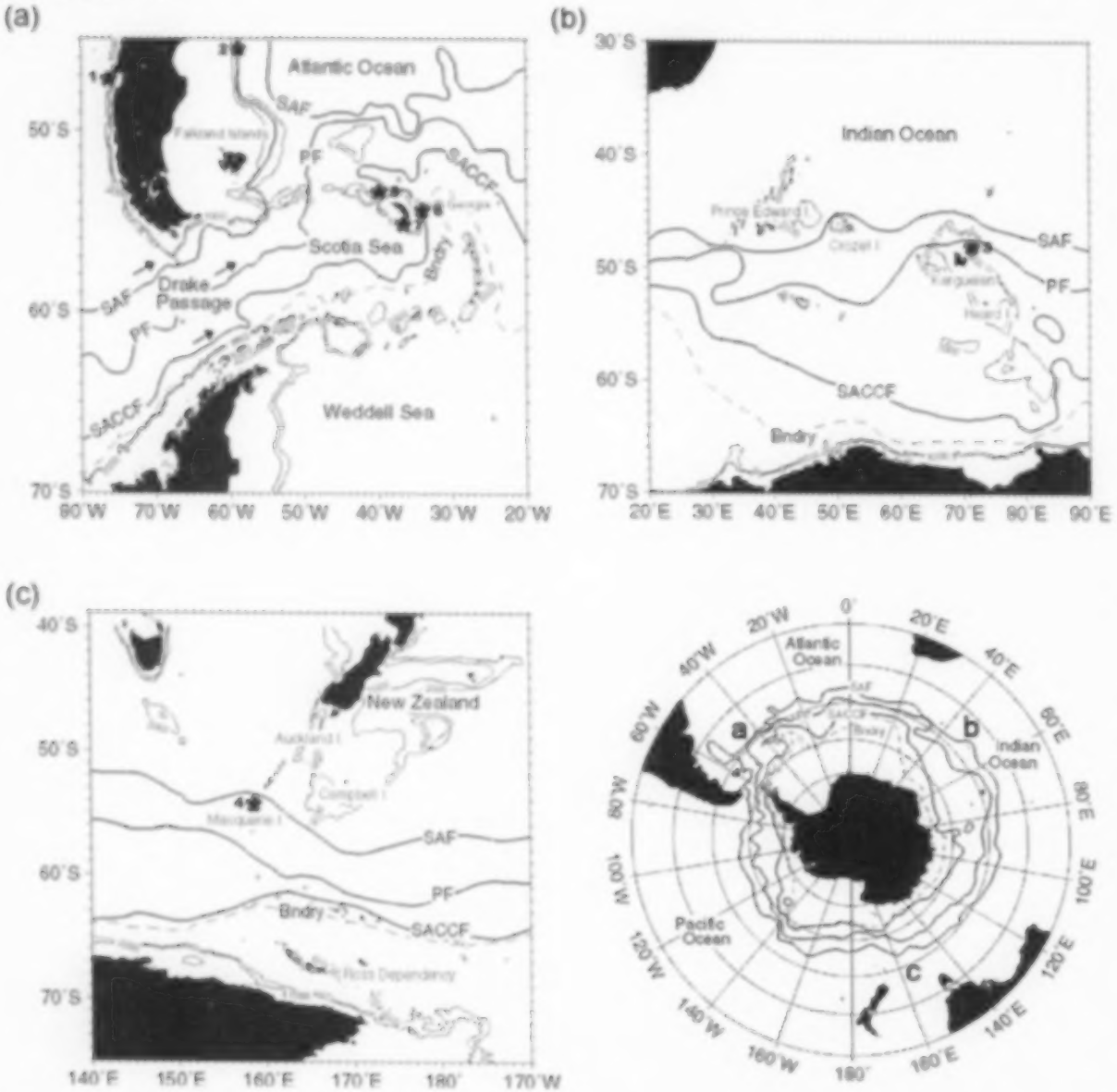
In the Southern Ocean, strong zonal wind stress acting on surface waters drives the Antarctic Circumpolar Current (ACC) eastward, and thermohaline variation generates a complex pelagic environment that is stratified in a polar–temperate direction and characterized by broad quiescent zones interspersed with fronts (Hofmann 1985; Orsi et al. 1995). The Subantarctic Front (SAF) and Polar Front (PF) penetrate the entire water column at the Drake Passage (Nowlin and Clifford 1982). They persist around the Antarctic continent, appearing stable where they flow over large bathymetric features (Hofmann 1985; Orsi et al. 1995; Rintoul and Sokolov 2001) (Fig. 1). Vertical stratification also varies spatially: Circumpolar Deep Water is more shallow towards the pole, whereas after sinking in the Polar Frontal Zone, Antarctic Intermediate Water is found at depth off South America. Differential exposure to trace elements from wind-driven, riverine, glacial, and geothermal sources, combined with biological processes and physical mixing downstream of sources, leads to environmental gradients in trace elements (e.g., Nolting et al. 1991; Westerlund and Öhman 1991).

Fish moving within this biogeochemical array may incorporate elements as spatially specific signatures in their otoliths that would provide a record of movement-at-age when combined with otolith chronology. Patagonian toothfish (*Dissostichus eleginoides*) are distributed on the continental shelves and shelf breaks of banks and island groups in the ACC and along western and eastern South America. They are bentho-pelagic tertiary predators (Eastman 1993) that attain a maximum total length of more than 2 m and live over 50 years (Ashford 2001; Horn 2002). They are managed as spatially discrete stocks within zones broadly corresponding to island groups under the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) and the Exclusive Economic Zones (EEZ) of neighboring national authorities. Consistent with spatial separation, genetic studies discounted panmixia and showed heterogeneity between management areas in different ocean basins (Smith and McVeagh 2000; Appleyard et al. 2002) and between South Georgia and the Falkland Islands (Shaw et al. 2004). However, rather than resulting from separation, this spatial heterogeneity may be the result of movement and mixing of populations in different proportions. This is difficult to discount using genetic approaches, however, because toothfish spawning areas are unknown and population-specific markers remain unidentified. On the other hand, management zones across the western Indian Ocean showed genetic homogeneity (Appleyard et al. 2004), suggesting a single population moving between seamounts and islands. But instead, this may reflect several populations, as movement of only a few fish between spatially discrete populations can counteract divergence through natural selection or genetic drift.

The evidence from tagging studies indicates that most recaptures were caught near the area of marking (e.g., Williams et al. 2002), consistent with spatial separation. However, tagging effort concentrated on sizes corresponding to immature fish, which are negatively buoyant in *D. mawsoni*, the congener of Patagonian toothfish (Eastman 1993; Near et al. 2003). It did not address early stages, which are pelagic (North 2002), or older stages in which *D. mawsoni* become neutrally buoyant at maturity, thereby considerably reducing

© 2005 NRC Canada

Fig. 1. Map of the Southern Ocean showing mean position of major fronts: SAF, Subantarctic Front; PF, Polar Front; SACCF, southern Antarctic Circumpolar Current Front; southern boundary (Bndry) of the ACC is shown as a broken line (Orsi et al. 1995). Detailed maps of the (*a*) Atlantic, (*b*) Indian, and (*c*) Pacific sectors of the Southern Ocean. Arrows show current direction. Sampling areas: 1, Chile, 1996; 2, Falkland Islands, 1997; 3, Kerguelen, 1996; 4, Macquarie, 1996; 5, South Georgia, 1996; 6, South Georgia, 1997; 7, South Georgia, 1998.



the energy needed to move using currents in the ACC (Ashford et al. 2003). Yet some tagged fish moved considerable distances (Williams et al. 2002), and similar size-at-age distributions between Kerguelen and South Georgia, despite differences in diet (Duhamel 1981, Goldsworthy et al. 2002), suggested that spatial differences due to growth may be homogenized by movement along the ACC (Ashford et al. 2003).

If it occurs, movement may be only of nonbreeding vagrants (Sinclair 1988), mixing in their new locality with resident fish that are reproductively active. Even so, a large rate of vagrancy will reduce the number of spawners in the source population, and arriving vagrants may inflate the apparent number of spawners at their destination area, carrying the risk of recruitment overfishing. Indeed, restriction of the breeding population may help explain strong differentiation in mtDNA where differences in nuclear DNA were not detected (Appleyard et al. 2002). Alternatively, if migrating fish return to breed in their natal population, variation in

© 2005 NRC Canada

their mortality or movement would directly affect spawning biomass. It is unlikely that this effect would be spatially uniform: some areas or habitats may be more critical to future recruitment than others.

To assess these questions using otolith chemistry, researchers need to reliably link signatures to geographic area. Once they are able to do so, they can begin to identify the provenance of captured oceanic fish from otolith material laid down earlier in the life history and hence study movement and use of critical habitat. The important first step, however, is to demonstrate that otoliths do, in fact, record spatially specific signatures. To test this, we compared otoliths taken from toothfish caught from five fishing management zones within two geographic regions around southern South America and in the Antarctic. In contrast to the analyses of whole otoliths and nucleus signatures undertaken previously for marine fish using ICP-MS, we used lasers to target the outer edges of otoliths, which specifically correspond to the environment occupied in the period immediately prior to capture, to validate the use of otolith chemistry in differentiating known marine habitats.

Materials and methods

Fishery observers collected otoliths between March and April 1996 from commercial catches of Patagonian toothfish taken in the Antarctic off the northern continental slope of South Georgia (United Nations Food and Agriculture Organization Statistical Subarea 48.3) and off the eastern continental slope of Kerguelen (Division 58.5.1), both situated on the Antarctic continental side of the PF in the southern Atlantic and Indian oceans, respectively (Fig. 1). Otoliths were also collected from Antarctic fish caught off the west coast of the Macquarie Island Exclusive Economic Zone (EEZ) located between the SAF and PF in the southern Pacific. For the region around South America, observers sampled fish from artisanal fishermen returning to Chiloe Island in the Chilean EEZ, north of the SAF. As fish could not be collected off the Falkland Islands in the same year, observers sampled again between April and May 1997 off the South American continental slope north of the Falkland Islands Conservation Zone (FCZ) and the eastern slope of South Georgia. Otoliths were also selected randomly from observer sample sets taken from the slope south of South Georgia in 1998. At each collection, female toothfish between 90 and 110 cm total length were sampled to minimize effects resulting from sex and life stage. Off Chile, otoliths could not be collected before removal of gonads by fishermen, and sex data were not recorded. All fish were taken from depths greater than 1000 m, except for those taken at Macquarie Island, where the depths were ~400–500 m.

Otoliths were dried and stored in envelopes and returned to the laboratory at Old Dominion University. One otolith was selected randomly from each pair, rinsed in milli-Q water, sonicated for 2 min, and rinsed again to remove any surface contamination. After drying, otoliths were ground from the anterior and posterior sides using a Hillquist Thin Section Machine (Hillquist Inc., Denver, Colorado) to produce thick transverse sections. Final processing was done in a class-100 clean room. We rinsed all remaining sections in milli-Q water under a laminar flow hood and lapped each manually using clean plastic clamps and Mark V Laboratory polishing film (Mark V Laboratory, East Granby, Connecticut). Each otolith was lapped successively on three pieces of clean 3 µm film and finished on 0.3 µm film. One otolith from each treatment was randomly selected and mounted in random order on a clean petrographic slide using silicon glue. Two otoliths were damaged during preparation and were not used in the analysis. The mounted sections were rinsed, sonicated for 5 min, then rinsed again twice, all in milli-Q water, and left to dry under a positive flow hood.

We used a Finnegan Mat Element 2 double-focusing sector-field ICP-MS located at the Laboratory for Isotope and Trace Element Research (LITER) at Old Dominion University (Norfolk, Virginia) to examine minor and trace element signatures. Instrument details are given in Jones and Chen (2003). Samples were introduced in automated sequence (Chen et al. 2000) using a New Wave Research EO LUV 266 laser ablation system and a PFA microflow nebulizer. Ablated otolith material from the sample cell was mixed in the spray chamber with an aerosol of 1% HNO_3 introduced by the nebulizer, and the mixture was then carried to the ICP torch. Laboratory calibration standards consisted of known-concentration multi-element solutions synthesized from stock single element standards and were similarly introduced to the spray chamber by the nebulizer as an aerosol before being carried to the ICP torch. Blanks of 1% HNO_3 aerosol also were introduced to the chamber by the nebulizer. For quality control, we used dissolved otolith reference material obtained from the National Research Council of Canada. To control for operational variability in the laser ICP-MS, a randomized blocks design was used with each petrographic slide as the blocking factor, considered randomly drawn, with each sampling area considered a fixed treatment. Blank and standard readings of count rate (counts·s^{-1}) were obtained before and after random presentation of the otolith sections in each block. Readings of reference material were obtained before sample presentation. To calculate element-to-Ca ratios (Me/Ca), background counts were subtracted from otolith counts by interpolating between readings taken before and after each block of otoliths, and the corrected otolith counts were converted to Me/Ca concentrations using the standards. To sample the edge, we used a line raster type with a laser beam of diameter 20 µm, frequency at 10 Hz, and power at 60%, travelling ~900 µm along the proximo-dorsal edge of the otolith section at 6 µm·s^{-1} and giving a predicted mean crater width of 17 µm and crater depth of 105.4 µm (Jones and Chen 2003). Dwell time was 15.0 ms.

Response variables were concentrations of Mg/Ca, Mn/Ca, Sr/Ca, and Ba/Ca. Overall, Ba/Ca and Sr/Ca showed a strong relationship implying some redundancy, but because the relationship was weak for southern Chile, both variables were included. We applied multivariate analysis of variance (MANOVA) and discriminant analysis (MDA) and used separate univariate analyses to examine the behaviour of each element. Multivariate outliers were identified by plotting robust squared Mahalanobis distances of the residuals (D_i^2) against the corresponding quantiles (Q–Q plot) of the chi-square distribution. We checked the assumption of multivariate normality analytically using tests ($\alpha = 0.05$) based on Mardia's multivariate skewness and kurtosis measures (Khattree and Naik 1999) and graphically using Q–Q plots

© 2005 NRC Canada

of squared Mahalanobis distances (d_i^2). As data were not normally distributed, we used a reciprocal transformation to fulfill the assumption of multivariate normality; univariate normality followed as a property of multivariate normality (Khattree and Naik 1999).

For the MANOVA, as variance–covariance matrices were not equal according to Bartlett's modification ($\chi^2 = 140.0$, df = 60, $\alpha = 0.10$), transformed data were normalized using the square root of the sample dispersion matrix for each area, allowing the sample mean vectors to float. We tested six contrasts for departures from null hypotheses of no differences in elemental concentrations, using an experimentwise $\alpha = 0.0083$. To test between fish caught in the region around South America versus the Antarctic region, we used the following contrasts: (*i*) 1996, Chile vs. south of SAF (South Georgia, Kerguelen, Macquarie); (*ii*) 1997, Falkland Islands vs. South Georgia. To test between the subset of sampling areas in the Antarctic, we used contrasts to test between treatments from 1996: (*iii*) South Georgia vs. Kerguelen; (*iv*) South Georgia vs. Macquarie; (*v*) Kerguelen vs. Macquarie. We also tested (*vi*) the northern slope (1996) vs. the eastern slope (1997) of South Georgia.

As the MANOVA indicated populations were distinguishable from each other, we proceeded to apply MDA. However, because variance–covariance matrices were not equal and pooled variance–covariance matrices were therefore inappropriate, we used individual variance–covariance matrices instead and applied quadratic MDA (Khattree and Naik 2000). The error rates were estimated by cross-validation, using equal prior probabilities. Finally, we examined the data using univariate analysis of variance (ANOVA) ($\alpha = 0.05$) on transformed data to detect the behaviour of individual elements, using pairwise comparisons with SNK tests. The assumption of homogeneity of variance was fulfilled for all concentrations except Mn/Ca.

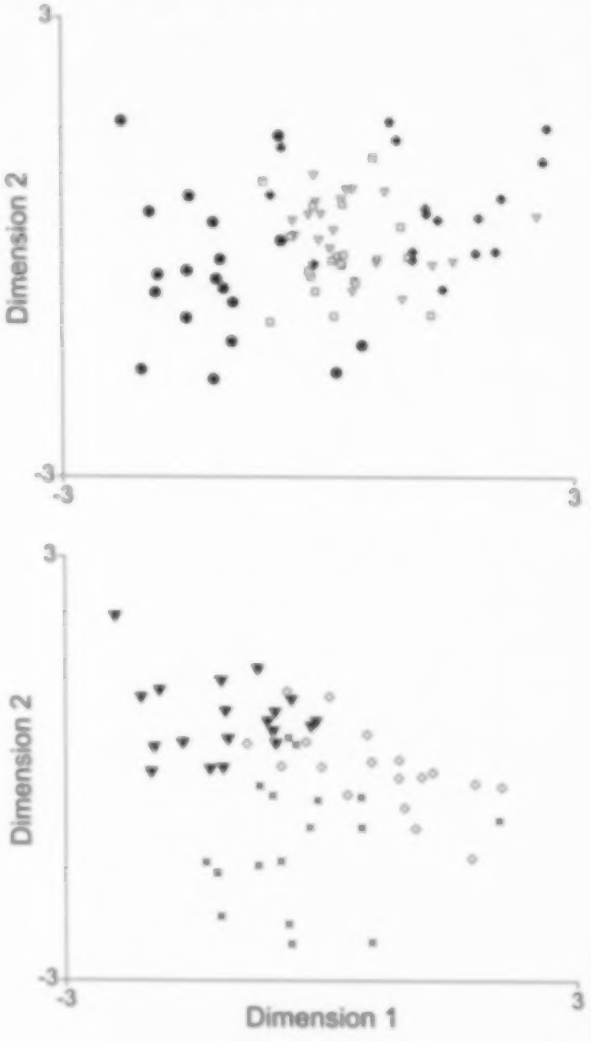
In addition to parametric statistics, we examined the data graphically using nonmetric multidimensional scaling (nMDS) (Kruskal and Wish 1978; Schiffman et al. 1981). Because the variables had different absolute magnitudes and ranges, they were standardized to the same scale. We constructed a dissimilarity matrix based on Euclidean distances from which we created a two-dimensional projection of distance between individual fish using a convergence criterion of Stress < 0.01.

Results

Otolith chemistry was significantly different between all comparisons. Multidimensional scaling showed strong separation between fish captured off South America and those captured in the Antarctic, plotted by year for clarity (Fig. 2). Fish taken off Kerguelen in 1996 showed considerable overlap with those from Macquarie Island, but fish from both sampling areas separated from those taken in the same year from South Georgia. South Georgia fish taken from the southern continental slope in 1998 clearly differentiated from those taken from the eastern slope in 1997.

The MANOVA showed significant differences between sampling areas (Pillai's Trace = 2.95, $F = 57.9$, $P < 0.0001$). Elemental signatures from toothfish caught off South America were significantly different from those of Antarctic fish

Fig. 2. Relationships between samples of Patagonian toothfish (*Dissostichus eleginoides*) taken from sampling areas in the Southern Ocean between 1996 and 1998, using nonmetric multidimensional scaling (nMDS) based on Euclidean distances. For clarity of illustration, samples are separated by year. (*a*) Samples taken in 1996: Chile, ●; Kerguelen, ▽; Macquarie, □. (*b*) Samples taken in 1997–1998: Falkland Islands, 1997, ▼; South Georgia, 1997, ◇; South Georgia, 1998, ×.



(Tables 1 and 2). We also detected significant differences between fish taken off South Georgia, Kerguelen, and Macquarie in 1996 and significant differences between fish taken off the northern and eastern continental slopes of South Georgia.

The univariate analysis showed significantly higher Sr/Ca values for fish from the Antarctic region compared with those off South America. Concentrations of Ba/Ca were significantly lower for the Falkland Islands than elsewhere, but significantly higher at South Georgia in 1996 than at other areas sampled that year. Fish from Chile and the Falkland Is-

© 2005 NRC Canada

Table 1. Concentrations of trace elements ratioed to Ca (μmol·mol^{-1}), sampled from the outer edge of the otoliths from Patagonian toothfish (*Dissostichus eleginoides*) taken in commercial fisheries at five different sites in the Southern Ocean.

Year	Site	*n*	Mean	CV
(*i*) Mg/Ca				
1996	Chile	19	75.1	0.61
	Macquarie	20	105.6	0.38
	South Georgia	17	44.1	0.51
	Kerguelen	20	67.4	0.47
1997	Falklands	19	54.6	0.31
	South Georgia	18	63.4	0.39
1998	South Georgia	17	290.9	0.73
(*ii*) Mn/Ca				
1996	Chile	19	2.79	2.06
	Macquarie	20	0.19	1.68
	South Georgia	17	0.15	0.56
	Kerguelen	20	0.13	0.73
1997	Falklands	19	0.79	0.69
	South Georgia	18	0.27	0.68
1998	South Georgia	17	1.59	1.09
(*iii*) Sr/Ca				
1996	Chile	19	3790	0.24
	Macquarie	20	5233	0.15
	South Georgia	17	6574	0.24
	Kerguelen	20	5520	0.25
1997	Falklands	19	3827	0.14
	South Georgia	18	6052	0.29
1998	South Georgia	17	5467	0.36
(*iv*) Ba/Ca				
1996	Chile	19	2.61	0.42
	Macquarie	20	2.65	0.38
	South Georgia	17	4.51	0.45
	Kerguelen	20	2.99	0.64
1997	Falklands	19	1.53	0.25
	South Georgia	18	3.84	0.59
1998	South Georgia	17	3.11	0.57

Note: CV, coefficient of variation.

Table 2. Contrasts from multivariate analysis of variance of Patagonian toothfish (*Dissostichus eleginoides*): (*i* and *ii*) samples taken off South America vs. those taken in the Antarctic in 1996 and 1997; (*iii*–*v*) between samples taken in the Antarctic in 1996; and (*vi*) samples taken from the northern vs. the eastern continental slopes of South Georgia in 1996 and 1997.

Comparison	Pillai's trace	*F*	Pr > *F*
(*i*) CH96 vs. SG, K, M96	0.926	373	<0.0001
(*ii*) FI97 vs. SG97	0.908	295	<0.0001
(*iii*) SG96 vs. K96	0.757	93	<0.0001
(*iv*) SG96 vs. M96	0.829	146	<0.0001
(*v*) K96 vs. M96	0.881	223	<0.0001
(*vi*) SG96 vs. SG97	0.853	175	<0.0001

Note: Dependent variables: Mg/Ca, Mn/Ca, Sr/Ca, Ba/Ca. α = 0.0083. Sites: CH, Chile; FI, Falkland Islands; K, Kerguelen; M, Macquarie; SG, South Georgia. "96" and "97" after the site codes refer to the years 1996 and 1997, respectively.

Table 3. Classification rates (%) from quadratic multivariate discriminant analysis undertaken for Patagonian toothfish (*Dissostichus eleginoides*) taken from sampling areas in the Southern Ocean, using four response variables (Mg/Ca, Mn/Ca, Sr/Ca, Ba/Ca).

	Area classified to						
Area sampled	CH	FI	K	M	SG96	SG97	SG98
CH	**84**	16	0	0	0	0	0
FI	5	**79**	11	0	0	5	0
K	0	5	**65**	10	10	10	0
M	0	0	25	**50**	5	10	10
SG96	0	6	12	6	**53**	23	0
SG97	0	5	11	5	11	**67**	0
SG978	6	0	6	23	6	6	**53**

Note: Sampling areas: CH, southern Chile, 1996 (n = 19); FI, Falkland Islands, 1997 (n = 19); K, Kerguelen, 1996 (n = 20); M, Macquarie, 1996 (n = 20); SG96, South Georgia, 1996 (n = 17); SG97, South Georgia, 1997 (n = 18); SG98, South Georgia, 1998 (n = 17). Bold values indicate rates of correct classification to sampling area.

lands had significantly higher concentrations of Mn/Ca than Antarctic fish in 1996–1997 but were not significantly different from fish taken in 1998 from the southern slope of South Georgia. Southern slope fish showed significantly higher Mg/Ca concentrations than all other samples, whereas fish caught off Macquarie Island showed significantly higher concentrations of Mg/Ca than all other 1996–1997 samples.

The quadratic MDA successfully classified fish to the region where they were captured: only four Antarctic fish were incorrectly classified to South American sampling areas and three South American fish were incorrectly allocated to Antarctic sampling areas. Within region, fish caught off South America were classified most successfully, with 79% of Falkland Island fish and 84% of fish from southern Chile correctly allocated (Table 3). Moreover, all misclassifications for Chilean fish were allocated to the Falkland Islands. Classification success for Antarctic fish was between 50% and 67%, but of the fish taken off the northern slope of South Georgia in 1996, half of the misclassifications were allocated to the nearest sampling area, on the eastern South Georgia slope in 1997. Similarly, half the misclassifications of Macquarie fish were to Kerguelen. Nevertheless, 67% of South Georgia eastern slope fish and 65% of Kerguelen fish were allocated correctly.

Discussion

Although previous researchers examined whole otoliths (Edmonds et al. 1989, 1991) and otolith nuclei (Campana et al. 1994) of marine fish, the present study uniquely used laser ICP-MS to place the otolith elemental signatures in their geographic context by examining material at the edge of the sectioned otolith, deposited in the interval immediately prior to capture. Edge signatures discriminated Patagonian toothfish caught off South America from those caught in the Antarctic with near-complete success, direct evidence that otolith elemental signatures of exclusively marine fish can record specific spatial locations. By extension, because oto-

© 2005 NRC Canada

lith material once deposited is not reworked (Campana and Neilsen 1985), otolith growth increments can record toothfish provenance at regional scales over the life history prior to capture, providing a means to measure movement directly and test hypotheses of population structure. In contrast, genetic markers can link fish only indirectly to geographic area at the time of spawning, and artificial tags are costly to use, are applied only to a proportion of the targeted population, and can link fish to geographic area only at the time of marking and recapture.

Moreover, strong differences between sampling areas within each region indicated edge signatures could record provenance at finer scales. With only four elements, 79%–84% of South American fish were correctly allocated to sampling area, success rates that compared favourably with the range reported for estuarine-dependent fish on the east coast of North America. Thus, juvenile weakfish (*Cynoscion regalis*) classified to their natal estuaries with 63% success using trace element data (Thorrold et al. 1998*a*), whereas American shad (*Alosa sapidissima*) classified to natal river with 90% success (Thorrold et al. 1998*b*). For Patagonian toothfish caught in the Antarctic, success rates were still comparable for Kerguelen fish and those caught off the eastern slope of South Georgia in 1997. Lower rates for fish from Macquarie and the northern and southern slopes of South Georgia were due largely to misclassification to a single other area, respectively, Kerguelen, the eastern South Georgia slope, and Macquarie, which may be resolved by the use of other chemical markers (Thorrold et al. 1998*a*). Even with only the markers used in this study, few South Georgia eastern slope fish were classified to the northern or southern slopes, and few of those caught along the southern slope were allocated to other South Georgia areas, suggesting that otolith chemistry may be capable of recording differences at spatial scales comparable to those achieved for spotted sea trout (*Cynoscion nebulosus*) within the Chesapeake Bay (Dorval et al. 2005).

However, the fact that Macquarie fish classified to Kerguelen at similar rates as northern slope to eastern slope fish at South Georgia argues that the discriminatory power of the signatures is not simply related to spatial distance, but instead reflects environmental gradients in trace and minor element concentrations. Thus, Mn is a scavenged element (Whitfield and Turner 1987), decreasing with depth in contrast to recycled elements like Ba. Deep-water flow patterns on a global scale mean that enrichment of recycled elements and uptake of scavenged elements along the direction of deep-water flow leads to fractionation between ocean basins (Donat and Bruland 1995). These larger trends are overlaid by finer-scale spatial differences between and within islands and seamounts.

For Ba, Dehairs et al. (1992) observed that barite accumulation in the open ocean of the ACC was generally associated with new production fueled by nitrate. Transport to depth occurred through surface uptake of dissolved Ba as barite particles ($BaSO_4$) in association with aggregates of biogenic debris. On sinking, the aggregates break down through bacterial activity, freeing enclosed barite crystals to accumulate at 200–700 m (Stroobants et al. 1991; Dehairs et al. 1997), where they settle slowly and dissolve at depth, consistent with the high mean otolith Ba/Ca found in the South Georgia toothfish in the present study. In contrast, Dehairs et al. (1992) found that continental shelf areas were associated with regenerated production dominated by ammonium uptake and little accumulated barite at depth, consistent with the low mean otolith Ba/Ca concentrations found in the Falkland Island fish.

For Mn, the thermodynamically stable form in oxidising seawater is insoluble Mn(IV), but Sunda and Huntsman (1988) suggested that photoreduction of Mn oxides and photoinhibition of Mn-oxidising microorganisms may maintain the dissolved Mn^{2+} maximum observed at the surface. Similarly, high dissolved Mn near the benthic layer where toothfish are caught is associated with effluxes from anoxic sediments. Upwelling has also been demonstrated in the wake of oceanic islands (e.g., Gordon et al. 1998); similarly, Bucciarelli et al. (2001) found the continental shelf zone to the northeast of Kerguelen to be influenced by enrichment from lithogenic origin and the resuspension of sediments. Off the eastern shelf slope, however, where Kerguelen fish were taken for the present study, they found that concentrations of dissolved Mn decreased abruptly offshore of the shelf front, below the surface layer and in association with Antarctic water. On the other hand, authigenic Mn activity recorded on the eastern side of South America (Anonymous 1989) is consistent with the higher concentrations of Mn/Ca in the otoliths of Falkland Island fish.

In contrast to estuaries, where Sr/Ca and Ba/Ca are inversely related because of the exchange of cations in seawater for Ba adsorbed on river-borne clays (Guay and Falkner 1998), Sr is quasiconservative in the oceanic environment: concentrations vary slightly, probably as a result of biogenic carbonate cycling (De Villiers 1999; Müller and de Deckker 2002). If this process were linked to barite formation (Bernstein et al. 1992), a common transport pathway to depth would help explain the relationship we found in toothfish between otolith Ba/Ca and Sr/Ca compared with the inverse relationship found in estuarine-dependent fish. It would also help explain the higher otolith Sr/Ca concentrations at Antarctic sampling areas compared with South American ones.

However, variation in ambient concentrations of oceanic Sr/Ca are at the limits at which otolith chemistry has so far been able to resolve experimentally (Bath et al. 2000). An alternative explanation is that Sr/Ca in toothfish otoliths is linked to physical variables such as salinity and temperature, but even though these drive the complex pelagic environment in the Southern Ocean, their variation at depth is small compared with shallower and more temperate regions. Temperature-dependent fractionation may behave differently at the lower temperatures encountered in the Southern Ocean (Townsend et al. 1992), but nevertheless, these ranges approach the demonstrated limits of resolution for otolith chemistry. For instance, the difference in temperature between warm Upper Circumpolar Deep Water and colder Bransfield Strait Water is in the order of 2 °C (Smith et al. 1999) compared with differences almost an order of magnitude greater between surface water types off the east coast of North America. Similarly, the difference between salinities found in Antarctic Winter Water and the salinity maximum in Lower Circumpolar Deep Water vary between only ~0.5 and 1.0 ppt. Instead, another explanation is that variation in

© 2005 NRC Canada

the rate of matrix protein formation linked to somatic growth may control otolith crystallization (Campana 1999), accounting for variation in otolith Sr/Ca concentrations. In consequence, divergent growth rates (Ashford 2001) could contribute to the differences in otolith Sr/Ca concentrations between the toothfish sampled in the present study off South America and that sampled in the Antarctic.

Thus, the spatial variation in toothfish otolith chemistry appears consistent with environmental structure in the Southern Ocean, mediated by physiological processes (Kalish 1989, 1991) such as growth that themselves vary spatially in rate. As a result, by empirically linking otolith elemental markers to geographic areas within a species' distribution, researchers can identify the provenance of captured oceanic fish over their entire life history and hence study their prior movement and use of critical habitat. Because otoliths also provide a chronology recorded in growth increments, these life history processes can be related to age and to calendar year when the capture date is known. Where elemental signatures can demonstrably discriminate areas of interest, these important advantages make otolith chemistry a valuable addition to the suite of tools available to study oceanic fish and a useful complement to older approaches employing genetic and artificial markers.

Acknowledgements

We thank the observers from CCAMLR, the Falkland Islands Fisheries Department, the Chilean IFOP, and the Universidad Austral de Chile for collecting the otoliths. We are grateful for the advice and support of Pedro Rubilar of the Universidad Austral de Chile, Dr. Conor Nolan, and the Falkland Islands Fisheries Department. We acknowledge Dr. Zhongxing Chen of the Chemistry Department at ODU for invaluable advice on the use of laser ICP-MS and Dr. Dayanand Naik of the Mathematics Department at ODU for statistical approaches. This work was supported through the British Antarctic Survey and the United States National Science Foundation (grant no. NSF-OPP-9614756).

References

Anonymous. 1989. Ocean chemistry and deep-sea sediments. Open University, Milton Keynes and Elsevier Science Ltd., Oxford, UK.

Appleyard, S.A., Ward, R.D., and Williams, R. 2002. Population structure of the Patagonian toothfish around Heard, McDonald and Macquarie Islands. Antarct. Sci. **14**: 364–373.

Appleyard, S.A., Williams, R., and Ward, R.D. 2004. Population genetic structure of Patagonian toothfish in the West Indian Ocean sector of the Southern Ocean. CCAMLR Sci. **11**: 21–32.

Ashford, J.R. 2001. In support of a rationally managed fishery: age and growth in Patagonian toothfish (*Dissostichus eleginoides*). Ph.D. dissertation, Old Dominion University, Virginia.

Ashford, J.R., Jones, C.M., Hofmann, E., Everson, I., and Duhamel, G. 2003. Is population structure of Patagonian toothfish (*Dissostichus eleginoides*) determined by the Antarctic Circumpolar Current? CCAMLR Sci. Paper No. WG-FSA-03/84.

Bath, G.E., Thorrold, S.R., Jones, C.M., Campana, S.E., McLaren, J.W., and Lam, J.W.H. 2000. Sr and Ba uptake in otoliths of marine fish. Geochim. Cosmochim. Acta, **64**: 1705–1714.

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B.S., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., and Weinstein, M.P. 2003. The role of nearshore ecosystems as fish and shellfish nurseries. Issues in Ecology No. 11. Ecological Society of America, Washington, D.C.

Bernstein, R.E., Byrne, R.H., Betzer, P.R., and Greco, A.M. 1992. Morphologies and transformations of celestite in seawater: the role of acantharians in strontium and barium geochemistry. Geochim. Cosmochim. Acta, **56**(8): 3273–3279.

Bucciarelli, E., Blain, S., and Treguer, P. 2001. Iron and manganese in the wake of the Kerguelen Islands (Southern Ocean). Mar. Chem. **73**: 21–36.

Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms, and applications. Mar. Ecol. Prog. Ser. **188**: 263–297.

Campana, S.E., and Neilsen, J.D. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. **42**: 1014–1032.

Campana, S.E., Fowler, A.J., and Jones, C.M. 1994. Otolith elemental fingerprinting for stock identification of Atlantic cod (*Gadus morhua*) using laser ablation ICPMS. Can. J. Fish. Aquat. Sci. **51**(9): 1942–1950.

Chen, Z., Canil, D., and Longerich, H.P. 2000. Automated in situ trace element analysis of silicate materials by laser ablation inductively coupled plasma mass spectrometry. Fresnius' J. Anal. Chem. **368**: 73–78.

Dehairs, F., Baeyens, W., and Goeyens, L. 1992. Accumulation of suspended barite at mesopelagic depths and export production in the Southern Ocean. Science (Washington, D.C.), **258**(5086): 1332–1335.

Dehairs, F., Shopova, D., Ober, S., Veth, C., and Goeyens, L. 1997. Particulate barium stocks and oxygen consumption in the Southern Ocean mesopelagic water column during spring and early summer: relationship with export production. Deep-Sea Res. Part II Top. Stud. Oceanogr. **44**(1–2): 497–516.

De Villiers, S. 1999. Seawater strontium and Sr/Ca variability in the Atlantic and Pacific oceans. Earth Planet. Sci. Lett. **171**: 623–634.

Donat, J.R., and Bruland, K.W. 1995. Trace elements in the oceans. *In* Trace elements in natural waters. *Edited by* B. Salbu and E. Steinnes. CRC Press, Boca Raton, Fla. pp. 247–281.

Dorval, E., Jones, C.M., Hannigan, R., and van Montfrans, J. 2005. Can otolith chemistry be used for identifying essential seagrass habitats for juvenile spotted seatrout, *Cynoscion nebulosus*, in Chesapeake Bay? Mar. Freshwater Res. **56**(5): 645–653.

Duhamel, G. 1981. Caracteristiques biologiques des principales especes de poisons du plateau continental des Iles Kerguelen. Cybium, 3e Sér., **5**(1): 19–32.

Eastman, J.T. 1993. Antarctic fish biology: evolution in a unique environment. Academic Press, San Diego, Calif.

Edmonds, J.S., Moran, M.J., and Caputi, N. 1989. Trace element analysis of fish sagittae as an aid to stock identification: pink snapper (*Chrysophrys auratus*) in Western Australian waters. Can. J. Fish. Aquat. Sci. **46**: 50–54.

Edmonds, J.S., Caputi, N., and Morita, M. 1991. Stock discrimination by trace-element analysis of otoliths of orange roughy (*Hoplostethus atlanticus*), a deep-water marine teleost. Aust. J. Mar. Freshwater Res. **42**: 383–389.

Goldsworthy, S.D., Lewis, M., Williams, R., He, X., Young, J.W., and van den Hoff, J. 2002. Diet of Patagonian toothfish (*Dissostichus eleginoides*) around Macquarie Island, South Pacific. Ocean. Mar. Freshwater Res. **53**: 49–57.

Gordon, R.M., Johnson, K.S., and Coale, K.H. 1998. The behaviour of iron and other trace elements during the IronEx-I and

© 2005 NRC Canada

PlumEx experiments in the Equatorial Pacific. Deep-Sea Res. **45**: 995–1041.

Guay, C.K., and Kenison Falkner, K. 1998. A survey of dissolved barium in the estuaries of major Arctic rivers and adjacent seas. Cont. Shelf Res. **18**: 859–882.

Hanski, I., and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* I.A. Hanski and M.E. Gilpin. Academic Press, San Diego, Calif. pp. 5–26.

Hofmann, E.E. 1985. The large-scale structure of the Antarctic Circumpolar Current from FGGE drifters. J. Geophys. Res. **90**(C4): 7087–7097.

Horn, P.L. 2002. Age and growth of the Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the New Zealand subantarctic to the Ross Sea, Antarctica. Fish. Res. **56**(3): 275–287.

Jones, C.M., and Chen, Z. 2003. New techniques for sampling larval and juvenile fish otoliths for trace-element analysis with laser-ablation sector-field inductively-coupled plasma mass spectrometry (SF-ICP-MS). *In* The Big Fish Bang: Proceedings of the 26th Annual Larval Fish Conference. *Edited by* H.I. Browman and A.B. Skiftesvik. Institute of Marine Research, Bergen, Norway. pp. 431–443.

Kalish, J.M. 1989. Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. J. Exp. Mar. Biol. Ecol. **132**: 151–178.

Kalish, J.M. 1991. Determinants of otolith chemistry: seasonal variation in the composition of blood plasma, endolymph and otoliths of bearded rock cod, *Pseudophycis barbatus*. Mar. Ecol. Prog. Ser. **74**: 137–159.

Khattree, R., and Naik, D.N. 1999. Applied multivariate statistics with SAS® software. 2nd ed. SAS Institute Inc., Cary, N.C.

Khattree, R., and Naik, D.N. 2000. Multivariate data reduction and discrimination with SAS® software. SAS Institute Inc., Cary, N.C.

Kruskal, J.B., and Wish, M. 1978. Multidimensional scaling. Sage Publications, Thousand Oaks, Calif.

Muller, A., and de Deckker, P. 2002. Magnesium, calcium and strontium in waters of the southern Tasman Sea at the confluence of the Indian, Pacific and Southern Oceans. Mar. Freshwater Res. **53**: 1115–1128.

Near, T.J., Russo, S.E., Jones, C.D., and DeVries, A.L. 2003. Ontogenetic shift in buoyancy and habitat in the Antarctic toothfish, *Dissostichus mawsoni* (perciformes: *Nototheniidae*). Polar Biol. **26**: 124–128.

Nolting, R.F., DeBaar, H.J.W., Van Bennekom, A.J., and Masson, A. 1991. Cadmium, copper and iron in the Scotia Sea, Weddell Sea and Weddell/Scotia Confluence (Antarctica). Mar. Chem. **35**: 219–243.

North, A.W. 2002. Larval and juvenile distribution and growth of Patagonian toothfish around South Georgia. Antarct. Sci. **14**(1): 25–31.

Nowlin, W.D., Jr., and Clifford, M. 1982. The kinematic and thermohaline zonation of the Antarctic Circumpolar Current at Drake Passage. J. Mar. Res. **40**: 481–507.

Orsi, A.H., Whitworth, T., and Nowlin, W.D. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep-Sea Res. Part I Oceanogr. Res. Pap. **42**(5): 641–673.

Polachek, T. 1990. Year round closed areas as a management tool. Nat. Res. Model. **4**: 327–354.

Pulliam, H.R. 1988. Sources, sinks and population dynamics. Am. Nat. **132**: 652–661.

Rintoul, S.R., and Sokolov, S. 2001. Baroclinic transport variability of the Antarctic Circumpolar Current south of Australia (WOCE repeat section SR3). J. Geophys. Res. **106**(C2): 2815–2832.

Schiffman, S.S., Reynolds, M.L., and Young, F.W. 1981. Introduction to multidimensional scaling: theory, methods, and applications. Academic Press, Orlando, Fla.

Shaw, P.W., Arkhipkin, A.I., and Al-Khairulla, H. 2004. Genetic structuring of Patagonian toothfish populations in the Southwest Atlantic Ocean: the effect of the Antarctic Polar Front and deep water troughs as barriers to genetic exchange. Mol. Ecol. **13**(11): 3293–3303.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle, Wash.

Smith, P., and M. McVeagh. 2000. Allozyme and microsatellite DNA markers of toothfish population structure in the Southern Ocean. J. Fish Biol. **57**(Supplement A): 72–83.

Smith, D.A., Hofmann, E.E., Klinck, J.M., and Lascara, C.M. 1999. Hydrography and circulation of the West Antarctic Peninsula Continental Shelf. Deep-Sea Res. Part I Oceanogr. Res. Pap. **46**: 925–949.

Stroobants, N., Dehairs, F., Goeyens, L., Vanderheijden, N., and Van Griecken, R. 1991. Barite formation in the Southern Ocean water column. Mar. Chem. **35**: 411–421.

Sunda, W.G., and Huntsman, S.A. 1988. Effect of light on redox cycles of manganese in the southwestern Sargasso Sea. Deep-Sea Res. **35**(8): 1297–1317.

Thresher, R.E. 1999. Elemental composition of otoliths as a stock delineator in fishes. Fish. Res. **43**: 165–204.

Thorrold, S.R., Jones, C.M., Swart, P.K., and Targett, T.E. 1998*a*. Accurate classification of juvenile weakfish (*Cynoscion regalis*) to estuarine nursery areas based on chemical signatures in otoliths. Mar. Ecol. Prog. Ser. **173**: 253.

Thorrold, S.R., Jones, C.M., Campana, S.E., McLaren, J.W., and Lam, J.W.H. 1998*b*. Trace element signatures in otoliths record natal river of juvenile American shad (*Alosa sapidissima*). Limnol. Oceanogr. **43**(8): 1826–1835.

Townsend, D.W., Radtke, R.L., Corwin, S., and Libby, D.A. 1992. Strontium:calcium ratios in juvenile Atlantic herring *Clupea harengus* otoliths as a function of water temperature. J. Exp. Mar. Biol. Ecol. **160**: 131–140.

Westerlund, S., and Öhman, P. 1991. Cadmium, copper, nickel, lead and zinc in the water column of the Weddell Sea, Antarctica. Geochim. Cosmochim. Acta, **55**: 2127–2146.

Whitfield, M., and Turner, D.R. 1987. The role of particles in regulating the composition of seawater. *In* Aquatic surface chemistry. *Edited by* W. Stumm. John Wiley and Sons, New York. pp. 457.

Williams, R., Tuck, G.N., Constable, A., and Lamb, T. 2002. Movement, growth and available abundance to the fishery of *Dissostichus eleginoides* Smitt, 1898 at Heard Island derived from tagging experiments. CCAMLR Sci. **9**: 33–48.

© 2005 NRC Canada

Ocean climate and El Niño impacts on survival of Cassin's Auklets from upwelling and downwelling domains of British Columbia

Douglas F. Bertram, Anne Harfenist, and Barry D. Smith

Abstract: We report on the survival of populations of Cassin's Auklet (*Ptychoramphus aleuticus*) that breed on two oceanic colonies in British Columbia: Triangle Island, near the northern end of the California Current Ecosystem, and Frederick Island to the north in the Alaska Current Ecosystem. We captured and banded birds at both colonies from 1994 to 2000 and analyzed the recovery data with the computer program MARK. Average local adult annual survival (± standard error) was significantly lower ($p = 0.0001$) on Triangle Island (0.71 ± 0.02) than that on Frederick Island (0.80 ± 0.02), likely a result of poor production in the California Current Ecosystem during the 1990s. Coincident with a strong El Niño event, survival in 1997–1998 fell in unison to the lowest values observed for both colonies (to 0.54 ± 0.05 and 0.64 ± 0.04, respectively, for adults). A common winter environment in the California Current Ecosystem could explain the unified mortality response of both British Columbia populations to an exceptionally poor food period. The seabird colonies in this study occupy key positions in relation to major oceanographic domains and hence provide unique platforms for investigations of marine ecosystem response to ocean climate variability in the Northeast Pacific Ocean.

Résumé : Notre étude traite de la survie des stariques de Cassin (*Ptychoramphus aleuticus*) qui se reproduisent dans deux colonies océaniques de la Colombie-Britannique, à l'île Triangle, près de l'extrémité nord de l'écosystème du courant de la Californie et à l'île Frederick, plus au nord dans l'écosystème du courant de l'Alaska. Nous avons capturé des oiseaux dans les deux colonies de 1994 à 2000 et les avons munis de bagues; nous avons analysé les données de recapture à l'aide du logiciel MARK. La survie annuelle moyenne locale (± erreur type) est significativement plus faible ($p = 0{,}0001$) à l'île Triangle (0,71 ± 0,02) qu'à l'île Frederick (0,80 ± 0,02), probablement à cause de la production réduite dans l'écosystème du courant de la Californie dans les années 1990. Durant un important événement El Niño en 1997–1998, la survie est tombée simultanément au niveau le plus bas observé dans les deux colonies (respectivement à 0,54 ± 0,05 et 0,64 ± 0,04 chez les adultes). Un environnement commun en hiver dans l'écosystème du courant de la Californie pourrait expliquer la réaction semblable de mortalité dans les deux populations de la Colombie-Britannique en réponse à une période exceptionnellement pauvre en nourriture. Les colonies d'oiseaux de mer de cette étude sont dans des positions clés par rapport aux domaines océaniques majeurs et elles fournissent donc des « plates-formes » exceptionnelles pour étudier la réaction des écosystèmes marins à la variabilité du climat océanique dans le nord-est du Pacifique.

[Traduit par la Rédaction]

Introduction

Recent climate variability in the Northeast Pacific Ocean has had major impacts on biological production and marine populations. During the warm phase of the Pacific Decadal Oscillation (a long-lived, El Niño-like pattern of Pacific climate variability; Mantua 2000; Mantua and Hare 2002), production of salmonids showed inverse patterns latitudinally, with poor production in the California Current Ecosystem and enhanced production in the Alaska Current Ecosystem (e.g., Hare et al. 1999; Botsford and Lawrence 2002). As upper trophic level predators, seabird populations in the Cali-

Received 21 September 2004. Accepted 11 July 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 8 November 2005.
J18318

D.F. Bertram.[1,2] Simon Fraser University, Centre for Wildlife Ecology, Department of Biological Sciences, 8888 University Drive, Burnaby, BC V5A 1S6, Canada, and Environment Canada, Canadian Wildlife Service, 5421 Robertson Road, Delta, BC V4K 3N2, Canada.
A. Harfenist[3] **and B.D. Smith.** Environment Canada, Canadian Wildlife Service, 5421 Robertson Road, Delta, BC V4K 3N2, Canada.

[1]Corresponding author (e-mail: bertramd@pac.dfo-mpo.gc.ca).
[2]Present address: Environment Canada, Canadian Wildlife Service, c/o Institute of Ocean Sciences, 9860 West Saanich Road, P.O. Box 6000, Sidney, BC V8L 4B2, Canada.
[3]Present address: Harfenist Environmental Consulting, P.O. Box 2498, Smithers, BC V0J 2N0, Canada.

 doi: 10.1139/F05-190 © 2005 NRC Canada

fornia Current have also reflected the recent warm ocean climate through negative impacts on survival (Bertram et al. 2000) and reproduction (Bertram et al. 2001; Gjerdrum et al. 2003; Abraham and Sydeman 2004). Indeed, seabirds are being increasingly recognized as a useful biological indicator and bellwether for marine ecosystem climate variability (Barbraud and Weimerskirch 2001; Boyd and Murray 2001) because of the breadth and variety of information that studies on seabirds can reveal. Most seabirds spend over 90% of their lives on the ocean and come ashore only to breed. Colony-based studies can provide estimates of timing of breeding, breeding effort, nesting performance (hatch and fledging success), and nestling growth and diet and can reveal insights about local production and marine community composition (e.g., Bertram et al. 2001). In addition, capture–mark–recapture (CMR) programs on colonies can yield information on age-specific annual survival, because seabirds are iteroparous, long-lived, tenacious to breeding colonies and nesting locations, and they can be individually marked. Because seabirds are migratory, variation in adult annual survival measured at the nesting colony may also reflect conditions at wintering areas that are distant from the breeding grounds. Gaston (2003) has reported that population changes may be determined by events on common wintering grounds for temperate and arctic populations of Thick-billed Murres (*Uria lomvia*). Opportunities for insights into seabird population dynamics in response to changes in marine ecosystems are heightened during extreme periods, such as the El Niño – La Niña event of 1997–1998. During the warm phase of the Pacific Decadal Oscillation and prolonged El Niño-like conditions during the 1990s (Trenbeth and Hoar 1996), surface waters in the California Current were anomalously warm, and sea surface temperatures peaked in 1998 during the 1997–1998 El Niño. Ocean temperatures cooled dramatically in 1999 coincident with the La Niña and a suspected regime shift to the cold phase of the Pacific Decadal Oscillation. Here we report on the impacts of ocean climate variability and the extreme events of the 1997–1998 El Niño (see Wolter and Timlin 1998) on two seabird populations in British Columbia (BC) with distinctly different oceanographic influences.

Within the Northeast Pacific Ocean, BC occupies a pivotal position from an oceanographic perspective, because the North Pacific Current (also called the West Wind Drift) bifurcates off its coast, forming the Alaska Current to the north and the California Current to the south. Associated with these major currents, BC has three oceanographic domains: the downwelling domain in the north, the upwelling domain in the south, and the transitional domain in the central coast (Ware and McFarlane 1989, Fig. 1). Queen Charlotte Sound, in the transitional domain, also provides an obstacle to poleward transport of water by disrupting the effectively continuous coastline that extends from central California to the northern tip of Vancouver Island.

BC supports large populations of colonial seabirds, including 75% of the world's Cassin's Auklet (*Ptychoramphus aleuticus*; Manuwal and Thoreson 1993*)* population, a largely planktivorous member of the family Alcidae, with breeding colonies widely separated by latitude. Cassin's Auklets are small seabirds (~180 g) that use their wings for flying and for propulsion underwater in search of prey. A Cassin's Auklet's maximum dive depth averaged 22 m with a mode of 40 m in a study at Reef Island, BC (Burger and Powell 1989). Seabirds tend to exhibit strong natal philopatry and breed at colonies from which they were hatched. Like most seabirds, Cassin's Auklets have long lives, delayed maturity, and low reproductive output (females usually lay a single egg per year on colonies in BC). Birds use underground burrows for nesting and only arrive and depart from the colony during darkness. The nestling is fed regurgitations each night from both parents, who carry food in a gular pouch. Foraging distances for breeders may be colony specific, with parents typically foraging within 30 km of Prince Island in California (Adams et al. 2004) and between 40 and 75 km from the colony on Triangle Island in BC (e.g., Boyd et al. 2000; Ryder et al. 2001). After the breeding season (March–July in BC), the birds migrate, leaving the colonies to return the following spring. Information on the marine areas used by BC's Cassin's Auklets during the nonbreeding season is extremely limited, but Campbell et al. (1990) and also Connie Smith (Simon Fraser University, Department of Biological Sciences, 8888 University Road, Burnaby, BC V5A 1S6, unpublished data) indicate that the birds winter along the Pacific Coast between southern Vancouver Island and Baja, California.

We report on differences in annual adult survival for Cassin's Auklet populations at two colonies in key positions with respect to the major currents and oceanographic domains within BC: Triangle Island at the northern end of the California Current in the upwelling domain and Frederick Island, influenced by the Alaska Current, in the coastal downwelling domain of BC (Fig. 1). The timing of the study (1994–2000) facilitated an additional natural experiment, because it allowed us to investigate the survival impacts of a major El Niño event during 1997–1998 on the two seabird populations. The contrast is interesting because despite distinct breeding colonies, the populations are migratory and both may winter at southerly locations in the California Current Ecosystem and thus share common marine environmental effects for part of the annual cycle. Finally, we discuss the utility for including seabird demographics in state-of-ocean investigations and reporting.

Materials and methods

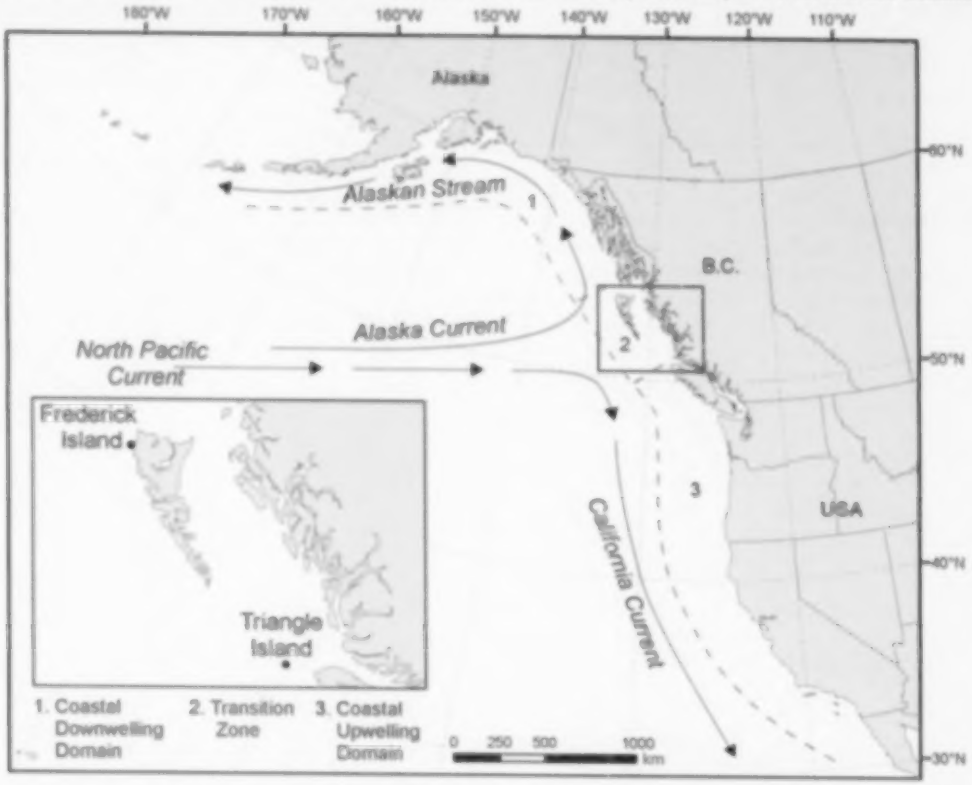
Study sites

The study sites are among the outermost western islands on the coast of BC in the Pacific Ocean near the continental shelf break, but are influenced by different oceanographic domains (Fig. 1). Triangle Island (51°52′N, 129°05′W), the largest seabird colony in BC and the largest Cassin's Auklet colony in the world (540 000 breeding pairs in 1989; Rodway et al. 1990), is windswept and effectively treeless as the outermost island of the Scott Island chain off the northern tip of Vancouver Island. The flora and fauna of the island have been described by Carl et al. (1951). The island is protected as an ecological reserve by the province of BC. Triangle Island was visited in all years 1994 to 2000.

Frederick Island (53°56′N, 133°11′W) lies approximately 2 km off the northwest coast of Haida Gwaii (Queen Char-

© 2005 NRC Canada

Fig. 1. Study sites showing major oceanographic domains and currents in British Columbia (after Ware and McFarlane 1989). Note that the north–south location of the bifurcation of the North Pacific Current can vary between years (Freeland and Cummins 2005).



lotte Islands). The colony had approximately 90 000 pairs of nesting Cassin's Auklets in 1980 (Rodway 1991). Frederick Island was visited in 1994–1998 and 2000. Frederick Island is largely forested; the vegetation is described in Rodway et al. (1994). The island is protected as a wildlife habitat area by the province of BC.

Cassin's Auklets were captured using barrier nets (5 cm × 5 cm multistrand plastic mesh) set at the base of nesting slopes (Triangle Island) or along the beach parallel to the edge of nesting areas (Frederick Island). Two trapping sites were used on each island. The sites were topographically isolated from each other and from sites of other concurrent studies (reproduction, diet, mate and site fidelity) on the islands, and no Cassin's Auklet banded in those other studies was caught in the traps. On Triangle Island, the net length and height were approximately 15 m × 3 m in West Bay and 20 m × 3 m in Calamity Cove. On Frederick Island, the Camp Bay net was approximately 40 m × 7.5 m, and the North Beach net was about 50 m × 8.5 m. Trapping was conducted from April to July on Triangle Island and from May to July on Frederick Island. We minimized disturbance to birds by trapping birds as they departed from the colony during the early morning after most arrivals had ceased. Nets were set between 0200 and 0500 on Triangle Island and from 0200 to 0530 or 15 min after the last bird was caught, whichever was later, on Frederick Island. Nets were set for 6–8 mornings at each site in each year on Frederick Island and for 10–20 mornings at each site on Triangle Island. We banded each bird caught with a United States Fish and Wildlife Service stainless steel band and scored iris colour based on modifications of the technique of Manuwal (1978; see below). On Frederick Island, most birds were released within 2 min of hitting the net. On Triangle Island, birds were measured and usually released within 2–20 min.

Burrow occupancy

To estimate breeding activity, we examined a sample of burrows each year for occupancy (presence of an egg, chick, or adult). Occupancy determinations were made throughout the incubation period on Triangle Island and during late incubation on Frederick Island coincident with the arrival of the field crew. When burrows were clearly defunct, new burrows were added to the sample. Our comparisons focused on differences between years within a colony rather than inter-colony contrasts in burrow occupancy.

CMR analysis

We prepared our banded bird resighting data from 1994 to 2000 for analyses of survival rates by the computer program MARK (White and Burnham 1999). Survival is an annual rate presumed to span the 365 days from the middle of the breeding period (approximately 15 May) in consecutive years. We cannot distinguish between breeding season and overwintering mortality, since the number of repeated sightings

© 2005 NRC Canada

of individuals in the short, spring breeding season was insufficient to calculate a meaningful survival rate. Survival was estimated using the Cormack–Jolly–Seber (CJS) model for marked individuals recaptured sequentially in time. Our intention to discriminate survival rates by location, age, and year, including the possible influence of an El Niño year, required that our data preparation consider three attributes of each Cassin's Auklet. For each Cassin's Auklet marked and recaptured, we recorded the location (trap site and island), the year, and the Cassin's Auklet's eye colour. Though the number of multiply recaptured birds was insufficient for breeding season survival analyses, these recaptures proved valuable for assessing the in-season reliability of eye colour assessments (see Appendix A).

Eye colour is a known index of Cassin's Auklet maturity, with iris colour evolving from brown, through mixed brown and white (which we term intermediate), then eventually to white as a Cassin's Auklet ages (Manuwal 1978; Emslie et al. 1990). However, eye colour is an imperfect index of age due to variability in the rate at which individual Cassin's Auklets progress from brown to white. Additionally, data accuracy is potentially complicated by the need to use a headlamp as a light source, which causes changes to pupil size and can make iris colour difficult to determine. To minimize measurement uncertainty in our assessment of eye colour, we recorded as many as six and four gradients in eye colour on Triangle and Frederick Islands, respectively, then later compressed these variants into the three less uncertain categories of brown, brown–white (intermediate), or white. Eye colour was easiest to score for white and brown-eyed birds and was most uncertain for the intermediate stages. We developed confidence that eye colour was a meaningful measure of Cassin's Auklet maturity and age by carefully following eye colour changes within and between seasons at both Triangle and Frederick islands (Appendix A).

Despite the need for caution when interpreting the intermediate eye colour category as a measure of age progression (see Results), we structured our CJS analysis on the premise that the eye colour of a Cassin's Auklet when it was first marked defined its age category at that time. We retained confidence in this protocol because our data strongly indicated that the duration of the intermediate eye colour was, on average, about 1 year (Appendix A). Thus for each of the two sites (s) on each of the two islands (i), our CJS analysis comprised three groups (g = 1, 2, A), each corresponding to eye colour at initial marking, resulting in a total of 12 groups. We then defined the corresponding age-structured, local survival rates, for first-year (a = 1, brown-eyed), second-year (a = 2, intermediate), and adult (a = A, white-eyed) birds, where local survival includes survivorship from both mortality and dispersal. Parameter matrices for each group were constructed to reflect this age progression and allow annual survival rates to differ among years (y, 1994–→1995 until 1999–→2000). Additionally, local survival rates for the first-year postmarking (m = 1), were allowed to differ from all later (m = L) annual local survival rates. This design feature allowed parametric distinction between estimates of local survival rates for birds that never returned the year after being marked (our so-called transients or prospectors) and estimates that measured survival of birds that returned at least once after having been marked (our so-called residents). We cannot interpret whether birds that never returned died or dispersed to other populations. We represent local survival (ϕ) and recapture probability (p) as thus $\phi_{i,g,m,a,y}$ and $p_{i,g,m,a,y}$.

As previously stated, no sampling on Frederick Island (F) was conducted during 1999, such that the recapture probability for 1999 is zero ($p_{F,g,m,a,1999} = 0$). We compensated for this missed sampling year in our analyses by assuming survival at Frederick Island to be unity from 1998–→1999 ($\phi_{F,g,m,a,1998\rightarrow1999} = 1$) then a posteriori interpreting the survival rates $\phi_{F,g,m,a,1998\rightarrow1999}$ and $\phi_{F,g,m,a,1999\rightarrow2000}$ to be identical as the square root of the estimate for $\phi_{F,g,m,a,1999\rightarrow2000}$.

Model parsimony was obtained by using a design matrix to minimize the potential number of model parameters (White and Burnham 1999). Preliminary analyses suggested similarities in the interannual patterns for ϕ among age classes for each island and site and similarities in the interannual patterns for p among eye colour groups for each island. Our hypothetical model set thus posed two models for p and three models for ϕ. Given the satisfactory performance of our global model for survivorship described above ($\hat{c}$ = 1.2), we thus limited our hypothesis concerning the vector of recapture probabilities, p, to two submodels: (*i*) an identity design and (*ii*) annual ps constrained to conform to similar patterns (pre-logit-transformation) for each group. Likewise, we limited our hypotheses concerning ϕ to four submodels: (*i*) a basic age–group structure but without a parametric accommodation for transient Cassin's Auklets, (*ii*) a basic age–group structure, (*iii*) a basic age–group structure but with the ϕs constrained to conform to similar patterns (pre-logit-transformation) for each group, and (*iv*) model *iii* but allowing the El Niño year to vary independently for the adult a = A age class.

Model selection protocols were followed as described in Burnham and Anderson (2002), with the best model (most parsimonious) being chosen on the basis of lowest Akaike's Information Criterion corrected over dispersion ($QAIC_c$). A posteriori goodness-of-fit diagnostics (including the coefficient of overdispersion $\hat{c}$) were evaluated to assure our analyzed data were a satisfactory realization of the model we accepted.

Results

Burrow occupancy 1994–2000

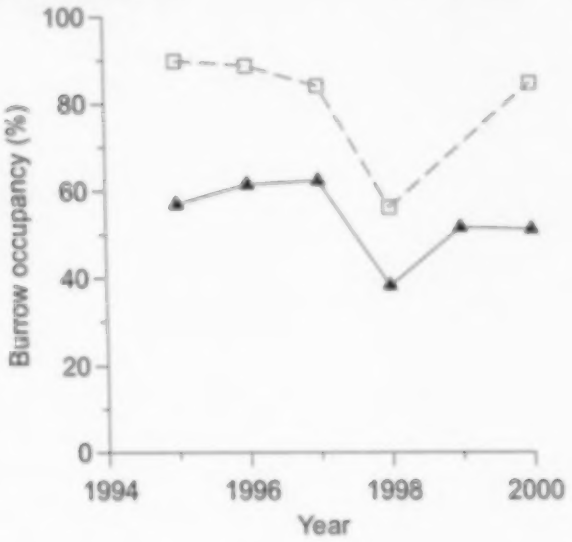
Burrow occupancy was consistently lower on Triangle Island than on Frederick Island in all years of the study from 1994 to 1998 (Fig. 2). Between 1994 and 1997, occupancy did not vary appreciably, averaging around 85% on Frederick Island and 60% on Triangle Island. In 1998, burrow occupancy fell by 20%–30% on both colonies to the lowest values recorded. Burrow occupancy increased following the El Niño on both colonies.

CMR analysis

A total of 1483 (at the Calamity Cove site) and 2050 (at the West Bay site) Cassin's Auklets were banded at Triangle Island. At Frederick Island, 1614 (at the Camp Bay site) and 1394 (at the North Beach site) Cassin's Auklets were

© 2005 NRC Canada

Fig. 2. Burrow occupancy (breeding propensity) on Triangle Island (triangles) and Frederick Island (squares). Note the drop in both colonies in 1998.



banded. Multiple recaptures within a year explain why fewer than these totals of birds contributed to the CMR analyses reported in Table 1.

Model ranking

Model ranking by $QAIC_c$ indicated that our best model (ranked 1st) supported three characteristics of our CMR data (Table 2). First, the phenomenon of having transient Cassin's Auklets that never returned to the particular site where they were marked was statistically validated. However, they may have returned to elsewhere on the island where they were marked. Second, there was a clear increase in the local survival rate as Cassin's Auklets aged. Third, there was support for the idea that interannual variability in survival was modulated similarly among the three age categories, with the exception of the El Niño year (Figs. 3 and 4; Table 3). Though there were unique features associated with each island, the general patterns of survivorship noted above pertained to both sites on both islands.

The complexity of the design matrix for the best model (1st ranked) tends to disguise the overall difference in survival rate between Frederick and Triangle islands because survivorship patterns vary with year, age, El Niño, and recapture sequence. To reinforce that there is an overall survivorship difference between the two islands, we refer to the 7th ranked model in Table 2. The age-structured survivorship and recapture parameters design matrix for this model is as described for our best model, with two exceptions: (*i*) there is no distinction between the two sites on each island, and (*ii*) adult survivorship is averaged over all years. When corrected for overdispersion ($\hat{c} = 1.39$), this model estimated the mean annual adult survival rate at Frederick Island (0.80 ± 0.02) to be substantially and significantly ($p = 0.0001$) higher than the survival rate at Triangle Island (0.71 ± 0.02).

Differences in survival and impacts of the 1997–1998 El Niño event

The distinction of the local survival rates for resident birds versus the local survival rates of transient birds is clearly portrayed (Fig. 3, residents; Fig. 4, transients). Survival estimates for resident adult birds were higher on Frederick Island (0.83 ± 0.02) than those on Triangle Island (0.77 ± 0.03) in non-El Niño years (5th-ranked model in Table 3; Fig. 3). The survival values were more similar between colonies for stage $a = 2$ birds, but the uncertainty in those estimates (standard errors, SEs) was much higher because of their smaller sample sizes and probably also because of imprecision in the assignment of age on the basis of eye colour. On both colonies, survival dropped markedly for all age classes during the 1997–1998 El Niño event (Table 3, Fig. 3). Despite the marked drop in survival on both colonies in 1997–1998, the intercolony differences persisted and Triangle Island showed a lower value for survival (0.54 ± 0.04) than that on Frederick Island (0.64 ± 0.03) during the El Niño.

Local survival rates for transient birds were markedly lower than the survival rates estimated for resident birds (Figs. 3 and 4), stabilizing at 0.1–0.6 after the 1994–1995 annual interval. The predominant pattern of increasingly lower local survival rates for increasingly younger birds at Frederick Island is consistent with the concept that the youngest birds are the least likely to have established a local site residency for reproduction. The less obvious pattern at Triangle Island is arguably due to the lesser precision in assessing eye colour at Triangle Island (Appendix A). At both Frederick and Triangle islands, there is a clear pattern of decreased local survival rates after the 1994–1995 interval. This phenomenon is an anomaly of the mark–recapture protocol and arises because most resident birds at a marking site were marked during the first year of marking. During that initial year, the ratio of resident to transient birds marked tends to be higher than in all subsequent years if the survival rate of the resident birds is high, as it is. Consequently, transient birds will predominate the selection of unmarked birds for marking in subsequent years and will dominate the estimate of local survival rates for the first year postmarking in those years. Interpretation of survival for these birds should focus on the estimates of these rates that have tended to stabilized over time, as appears to have happened for our data (Fig. 4; see also Bertram et al. 2000).

Discussion

Cassin's Auklets may be impacted by oceanic conditions at their breeding grounds and (or) their wintering grounds. The survival estimates presented here reflect cumulative impacts of mortality from both the breeding and nonbreeding seasons. Our results are consistent with the interpretation that the observed intercolony differences in adult annual survival were related to differences in prey availability near the breeding colonies, whereas the parallel drop in survival at both colonies during the 1997–1998 El Niño was associated with poor prey availability on common wintering grounds.

© 2005 NRC Canada

Table 1. Number of marked Cassin's Auklets (*Ptychoramphus aleuticus*) in each year contributing to the recovery matrix ($R(i,.)$, White and Burnham (1999)) for Frederick Island and Triangle Island.

Occasion	Marked	$R(i,.)$	j=1995	j=1996	j=1997	j=1998	j=1999	j=2000
Frederick Island[a]								
i=1994	797	797	503	70	18	7	0	0
i=1995	768	1271		581	75	23	0	10
i=1996	426	1077			507	55	0	29
i=1997	468	1068				292	0	91
i=1998	164	541					0	226
i=1999	0	0						0
Triangle Island[b]								
i=1994	931	931	392	73	23	16	11	4
i=1995	715	1107		272	78	38	8	5
i=1996	290	635			193	47	9	5
i=1997	506	800				128	27	13
i=1998	342	571					113	39
i=1999	453	621						113

[a]Total number marked = 2623. Effective sample size = 4754.
[b]Total number marked = 3237. Effective sample size = 4665.

Table 2. Model rankings and ranking criteria from the computer program MARK (White and Burnham (1999) for the predominant hypotheses posed to explain Cassin's Auklet (*Ptychoramphus aleuticus*) survival from 1994 to 2000 at Frederick Island and Triangle Island, B.C.

Model	Rank	$\Delta QAIC_C$	K	QDeviance	$\hat{c}$
Described age structure + El Niño[a]; p grouped by eye colour within sites (s)	1	0	88	798.61	1.23
Described age structure; p grouped by eye colour within sites (s)	2	2.65	84	809.47	1.23
Described age structure; identity p	3	22.36	110	776.09	1.24
Global model ($\phi_{(i,g,m,s,t)}$, $p_{(i,g,m,s,t)}$)	4	62.37	164	704.88	1.22
Described age structure with sites (s) combined within each island and adult survivorship averaged over all non-El Niño years; p grouped by eye colour within sites (s)	5	107.96	64	906.57	1.35
Described age structure with sites (s) combined within each island; p grouped by eye colour within sites (s)	6	114.44	62	913.05	1.35
Described age structure with sites (s) combined within each island and adult survivorship averaged over all years; p grouped by eye colour within sites (s)	7	148.07	62	946.67	1.39
Described age structure; no age a = A transients; p grouped by eye colour within sites (s)	8	346.14	78	1165.18	1.89
Described age structure; no a = A transients; identity p	9	357.64	100	1131.83	1.91

Note: Though simultaneously analysed, no parameters were shared by the Frederick Island and Triangle Island data sets. Akaike's Information Criterion corrected for over dispersion ($QAIC_C$) is based on $\hat{c}$ = 1.227 for the best (i.e., 1st-ranked) model. QDeviance, is the $\hat{c}$-corrected model deviance.
[a]This model was the most parsimonious among a few competitive parameterizations of the effect of an El Niño year on adult Cassin's Auklet mortality.

Consistent intercolony differences in adult annual survival

Adult Cassin's Auklet annual survival on Frederick Island (0.80 ± 0.02) was consistently higher than that on Triangle Island (0.71 ± 0.02) during our study. We suggest that the adult survival on Triangle Island is lower because the birds spend both winter and summer in the California Current, whereas the Frederick Island birds move further north to spend the breeding season close to the Alaska Current in a separate oceanographic domain. Poorer feeding conditions around Triangle Island can be inferred from nestling performance data from the two colonies; chick growth and production were consistently higher on Frederick Island from 1994 to 1998 (e.g., mean nestling growth rates (g·day^{-1}) between 5 and 25 days on Frederick vs. Triangle islands were as follows by year: 1994, 5.0 vs. 4.5; 1995, 5.2 vs. 5.0; 1996, 5.6 vs. 3.6; 1997, 5.7 vs. 4.9; 1998, 5.5 vs. 3.7). (Detailed comparisons of nestling production and diet on Triangle and Frederick islands are the subject of forthcoming work.) Poor nestling growth and production on Triangle Island have been linked to the timing and availability of high quality prey, the copepod *Neocalanus cristatus*, in surface waters around the Triangle Island colony (Bertram et al. 2001; Hedd et al. 2002). Increased provisioning effort of seabird parents in sustained years of poor prey availability can indirectly influence adult survival based on life history models developed from theory and empirical data (Erikstad et al. 1998). Experimental manipulation of the costs of chick rearing have demonstrated significant survival costs of chick rearing in Black-legged Kittiwakes (*Rissa tridactyla*; Jacobson et al. 1995; Golet et al. 1998). In addition, seasonal declines in body condition have been shown to be more pronounced in

© 2005 NRC Canada

Fig. 3. Estimates of annual local survival from the 1st-ranked model in Table 2 for the adult (a = A, solid lines) and intermediate (a = 2, broken lines) stages of Cassin's Auklets (*Ptychoramphus aleuticus*) at (*a*) Camp Bay and (*b*) North Bay on Frederick Island and at (*c*) Calamity Cove and (*d*) West Bay on Triangle Island. These estimates apply to annual intervals later than the first year after banding to distinguish the local survival estimates for these resident Cassin's Auklets from the local survival estimates for the first-year postmarking of transient or prospecting birds, which include losses due to permanent emigration.

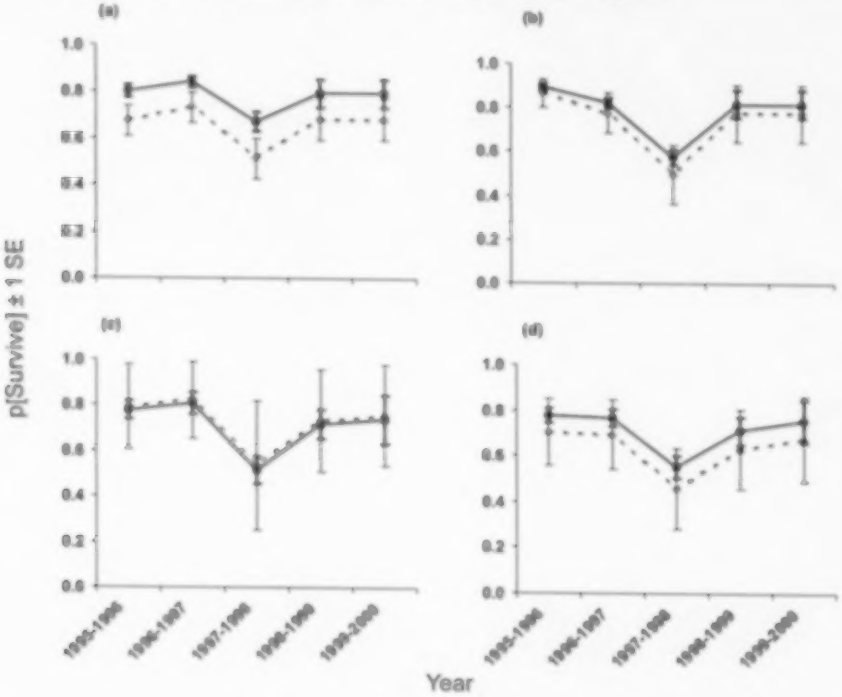


Table 3. Survivorship estimates (± approximate ĉ-corrected standard errors) by age class for a single El Niño year (1997–1998) and averaged over 4 non-El Niño years (1995–1996 to 1999–2000) (5th-ranked model) and all years combined (7th-ranked model) for Cassin's Auklets (*Ptychoramphus aleuticus*) at Frederick Island and Triangle Island, B.C.

	Frederick Island		Triangle Island	
Age class	Non-El Niño years	El Niño year	Non-El Niño years	El Niño year
a = 1[a]	0.17±0.02	0.07±0.02	0.29±0.08	0.13±0.05
a = 2[a]	0.73±0.06	0.48±0.08	0.74±0.14	0.51±0.19
a = A[a]	0.83±0.02	0.64±0.03	0.77±0.03	0.54±0.04
a = A[b]	0.80±0.02		0.71±0.02	

Note: Survivorship estimates reported for ages a = 2 and a = A are based on birds which had returned to be observed their first year after being marked (Fig. 3). These birds are presumed to be resident such that local survival estimates are considered to primarily represent mortality. Local survival estimates reported for age a = 1 include large losses due to both mortality and permanent emigration for so-called transients or prospectors (Fig. 4).

[a]Model ranked 5th in Table 2.
[b]Model ranked 7th in Table 2.

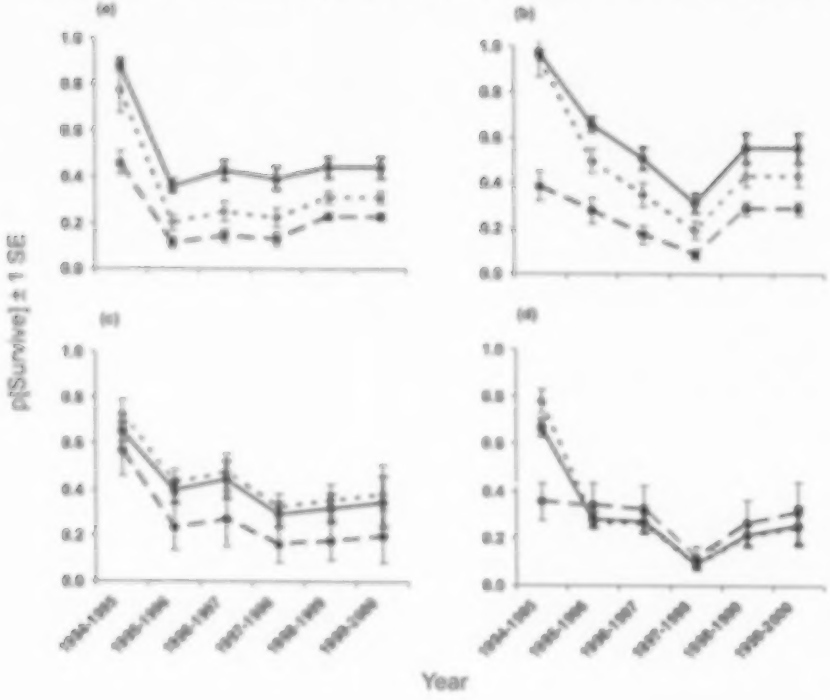
birds at "food-poor" than at "food-rich" colonies (Kitaysky et al. 1999).

As small seabirds, Cassin's Auklets likely spend much of their time foraging to meet their energetic requirements (Furness and Ainley 1984). They have been estimated to require 67% of their body mass per day in euphausids during chick rearing (Hodum et al. 1998). Thus, it is plausible that during the years of poor reproductive performance and reduced availability of the highly profitable copepod *N. cristatus* at Triangle Island, adult survival at that colony could be impacted through effects on body condition of breeders more than that on Frederick Island, where reproductive performance was consistently strong.

Cassin's Auklets also breed on the Farallon Islands in a colony of fewer than 20 000 pairs, situated in the central California Current off northern California. Low adult survival on the Farallon Islands (0.7 ± 0.02 from 1972 to 1997; Nur et al. 1998) during a period that overlaps the period of

© 2005 NRC Canada

Fig. 4. Estimates of annual local survival from the 1st-ranked model in Table 2 for adult (a = A, solid lines), intermediate (a = 2, dotted lines), and first-year (a = 1, broken lines) Cassin's Auklets (*Ptychoramphus aleuticus*) at (*a*) Camp Bay and (*b*) North Bay on Frederick Island and at (*c*) Calamity Cove and (*d*) West Bay on Triangle Island. These estimates apply only to the first year after banding to distinguish the confounding of dispersal within the local survival estimates for these transient or prospecting birds during the first-year postmarking from the survival estimates for our resident Cassin's Auklets. The figures for Frederick Island portray the tendency for younger birds to be less likely to return to the local site where they were marked when compared with older birds.



our study supports the conclusion that oceanic condition, rather than colony size, is the main cause of the differences in survival between Triangle and Frederick islands. The declines of Cassin's Auklet breeding populations on the Farallon Islands (Ainley et al. 1996; Nur et al. 1998; see also Pyle 2001), on Triangle Island (Bertram et al. 2000), and in wintering seabird populations in the Californian Current (Veit et al. 1996; Oedekoven et al. 2001) are likely attributable to large-scale declines in zooplankton production in the California Current (Roemmich and McGowan 1995; McGowan et al. 1998). In contrast, there is no evidence of population decline on Frederick Island between 1980 and 1998 (M. Lemon, Canadian Wildlife Service, 5421 Robertson Rd., Delta, BC V4K 3N2, Canada, unpublished data). It is worth noting that adult annual survival of the planktivorous Least Auklet (*Aethia pusilla*) from Buldir Island in Alaska between 1990 and 2000 was high and averaged 0.87 over the study period (Jones et al. 2002).

The annual adult survival for Cassin's Auklet from Triangle Island was previously estimated to be 0.67 based on data from 1994 to 1997 (Bertram et al. 2000). The value reported here of 0.71 is higher and more robust because the longer time series provides a greater probability of detecting birds that were alive but not recaptured during shorter intervals.

In contrast with the consistent intercolony differences in adult survival reported in this study, survival values were similar between colonies for stage a = 2 birds, most of which were likely not breeders (Pyle 2001). The uncertainty (SEs) in estimates for the intermediate birds was much higher because of their smaller sample sizes and probably also because of imprecision in the assignment of age on the basis of eye colour. Nonetheless, if survival was affected by provisioning effort by breeding adults, we would not necessarily expect to find a difference in survival of nonbreeders between Triangle and Frederick islands.

Independent evidence on growth and food consumption rate of planktivorous juvenile coho salmon (*Oncorhynchus kisutch*) from northern (north of 52°N) and southern BC (the area west of Vancouver Island, 47°N–51°N) match (Trudel et al. 2003) the patterns of seabird reproductive performance on Triangle Island (very poor) and Frederick Island (good) observed during the 1998 El Niño event. In 1998, coho salmon caught at the end of the growing season were about twofold smaller in southern BC (~200 g) than those in northern BC (~400 g). The lipid concentration was also lower for coho caught in southern BC in 1998. No differences in food consumption rates of coho could be detected among years (1998–2002), but changes in zooplankton community structure were much more pronounced in southern BC than in northern BC in 1998 (Trudel et al. 2003). The authors argued that the observed differences in juvenile coho growth rates in 1998 were likely due to differences in prey quality

© 2005 NRC Canada

mediated through changes in zooplankton community composition. Limited availability of high quality prey in 1998 was also the explanation proposed for retarded nestling growth and mortality for Cassin's Auklet on Triangle Island in that year (Bertram et al. 2001; Hedd et al. 2002).

Reduced survival during the 1997–1998 El Niño event

A striking result of our study was that the parameterization for our best model included a uniform drop in local survival for age $a = 2$ and older ($a = A$) categories of Cassin's Auklets on both Triangle and Frederick islands during the 1997–1998 El Niño event. Consistent with that observation was a reduction in burrow occupancy on both colonies in the 1998 breeding season.

We hypothesize that this drop reflects poor winter survival in 1997–1998 caused by food shortages for Cassin's Auklets from both colonies on their wintering grounds in the California Current Ecosystem (from mid Baja California to the northern end of Vancouver Island). Ocean production and zooplankton populations were greatly reduced during the winter of 1997–1998 throughout the California Current Ecosystem. In central California, the high-nutrient, productive waters that occur in a north–south band from the coast to approximately 200 km offshore during cool years disappeared during the El Niño. During the 18-month period of the El Niño, nitrate in surface waters was less than 20% of normal, and new production was reduced by 68%. Chavez et al. (2002) calculated the reduction in coastal California primary productivity associated with El Niño to be 50 million metric tons of carbon (5×10^{13} g C) and further stated that "this reduction certainly had deleterious effects on zooplankton, fish and marine mammals" (Chavez et al. 2002). In BC, time series data on zooplankton biomass and community composition before, during, and immediately after the 1997–1998 El Niño event were collected off southern Vancouver Island seaward from the shelf break to ~200 km offshore (Mackas and Galbraith 2002). During 1997–1998, zooplankton exhibited lower total biomass and shifts in community composition to more southerly fauna. The response was similar on the Oregon coast (Peterson et al. 2002; see also Mackas et al. 2004) and suggests that there was alongshore continuity from Oregon to southern BC in both oceanic forcing and zooplankton response to the recent El Niño event (Mackas and Galbraith 2002).

The similarity in the observed drop in Cassin's Auklet survival in birds from both Triangle and Frederick islands suggests that the impact was mediated in the wintering grounds and not caused by food shortages near the breeding colonies. Although evidence indicates that ocean productivity near Triangle Island was reduced during the spring and summer, no corresponding effect was evident near Frederick Island. In contrast with the situation in the California Current during the El Niño, zooplankton biomass and species composition in the Gulf of Alaska showed little interannual variation between 1997 and 2000 (Coyle and Pinchuk 2003). Furthermore, there was no drop in chick growth or fledging success in 1998 on Frederick Island (A. Harfenist, unpublished data), suggesting that prey availability was high around that colony, similarly to other years when breeding performance was also strong.

Supporting evidence for the idea that winter mortality in the California Current produced the observed survival patterns in 1997–1998 for Cassin's Auklets from Triangle and Frederick islands comes from the long-term research on the species from the Farallon Islands in central California. Analyses of time series data (1982–2002) revealed generally reduced survival during El Niño months (Sydeman and Lee 2003) and, in particular, a similar large decline in survival as observed for the BC populations during the 1997–1998 El Niño event (Abraham and Sydeman 2004; W.J. Sydeman, Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 949790, USA, personal communication). Most birds that breed on the Farallon Islands are believed to winter locally in the California Current Ecosystem (Manuwal and Thoresen 1993) and thus would have been exposed to the same poor foraging conditions as were the birds from BC.

In the spring of 1998, breeding was delayed on both Triangle and Frederick islands, perhaps because adults were in poor condition following a lean winter. The hatch dates of nestlings were 6 days later on Triangle Island in 1998 than the average date of the previous 4 years (Bertram et al. 2001) and 5 days later on Frederick Island than the average date of the previous 4 years (A. Harfenist, unpublished data). There is, however, no evidence that production at lower trophic levels was late in BC in 1998. The year 1998 was the earliest between 1994 and 1999 for the spring phytoplankton bloom peak (D. Ware, Aquatic Ecosystem Associates, 3674 Planta Road, Nanaimo, BC V9T 1M2 Canada, personal communication), and the spring peak of *N. cristatus*, a key component of the diet of BC's Cassin's Auklets (Vermeer 1981; Bertram et al. 2001), was also early off the west coast of Vancouver Island (Mackas and Galbraith 2002). Delayed breeding is also reported for Cassin's Auklets during El Niño years in the Farallon Islands (Ainley et al. 1990; Abraham and Sydeman 2004).

Long-term ecosystem monitoring at sentinel colonies of planktivorous seabirds

Our results demonstrate marked survival differences between seabird populations breeding within different oceanographic domains in BC. Our data, coupled with independent data for juvenile salmonids, indicate that BC is a pivotal location for detecting major oceanographic influences on upper trophic level predators. Our results on survival show that Cassin's Auklet populations performed better in the north than in the south and that both responded rapidly and strongly to the 1997–1998 El Niño event. In 1999, Cassin's Auklet breeding performance improved significantly on Triangle Island, demonstrating a rapid response to the abrupt changes in regional zooplankton communities in that year (Bertram et al. 2001; Hedd et al.2002; see also Mackas et al. 2001). We suggest that survival and reproduction parameters of planktivorous seabirds may respond more directly and rapidly than those of piscivorous seabirds to ocean climate variation because (*i*) small body size and high daily energy demand increase foraging time commitments and heighten reproductive sensitivity to lean periods, (*ii*) the trophic connection between zooplankton and seabirds is direct, and (*iii*) many zooplankton prey have annual life cycles, whereas overlapping cohorts of prey fish could serve to buffer poor

© 2005 NRC Canada

food years if birds can exploit a variety of fish age classes. In contrast with Cassin's Auklet, the larger, piscivorous Rhinoceros Auklet (*Cerorhinca monocerata*) from Triangle Island showed no survival impact from the 1997–1998 El Niño event (B.D. Smith, unpublished analysis). The traits of iteroparity and breeding site fidelity facilitate many years of returns from individually marked seabirds. Demographic studies on seabirds that measure adult survival, reproductive performance, and diet provide insights to marine ecosystems at local (within 100 km of breeding colonies) and broader scales within the migratory range during the nonbreeding season. Integration of regional fisheries and biological, oceanographic investigations with seabird time series data from sentinel colonies, such as those on Triangle Island and Frederick Island, could provide a bellwether for future ecosystem changes in the Northeast Pacific Ocean.

Acknowledgements

We thank the many volunteers and field assistants on both islands. We especially acknowledge Rob Kelly and Mark Drever on Frederick Island and crew leaders Laura Cowen, Hugh Knechtel, and John Ryder on Triangle Island for their major efforts. We thank the Canadian Coast Guard for ship and helicopter support on Triangle Island. Special thanks go to Henry Hageman of the *Elnack 3*, who piloted crew and supplies to Frederick Island. Ian Jones and Fred Cooke initiated the demographic study on Triangle Island. Thanks go to Connie Smith for organizing the banding data sets, reporting, and assistance with permits and to Marianne Ceh for creating the map. Gary Kaiser (Canadian Wildlife Service (CWS)) provided key logistic and technical support. BC Parks granted permission to work on the Anne Vallée Ecological Reserve, Triangle Island. The Council of Haida Nations approved the research activities on Frederick Island in Duu Guusd Tribal Park. We acknowledge the CWS, Natural Sciences and Engineering Research Council of Canada (NSERC) grants to Fred Cooke, and support funds from Centre for Wildlife Ecology at Simon Fraser University. Grants from the Nestucca Oil Spill Trust Fund and the Canadian Climate Change Action fund to D.F.B. and a collaborative United States National Oceanographic and Atmospheric Administration (US NOAA) grant in 1998 (NA77RJ0453) led by W.J. Sydeman are gratefully acknowledged.

References

Abraham, C.L., and Sydeman, W.J. 2004. Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, *Ptychoramphus aleuticus*. Mar. Ecol. Prog. Ser. **274**: 235–250.

Adams, J., Takekawa, J.Y., and Carter, H.R. 2004. Stable foraging area and variable chick diet in Cassin's auklets (*Ptychoramphus aleuticus*) off southern California. Can. J. Zool. **82**: 1578–1595.

Ainley, D.G., Boekelheide, R.J., Morrell, S.H., and Strong, C.S. 1990. Cassin's Auklet. *In* Seabird of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community. *Edited by* D.G. Ainley and R.J. Boekelheide. Stanford University Press, Stanford, Calif. pp. 306–338.

Ainley, D.G., Spear, L.B., and Allen, S.G. 1996. Variation in the diet of Cassin's auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, USA. Mar. Ecol. Prog. Ser. **137**: 1–10.

Barbraud, C., and Weimerskirch, H. 2001. Emperor penguins and climate change. Nature (London), **411**: 183–186.

Bertram, D.F., Mackas, D.L., and McKinnell, S.M. 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. Prog. Oceanogr. **49** : 283–307.

Bertram, D.F., Jones, I.L., Cooch, E., Knechtel, H., and Cooke, F. 2000. Survival rates of Cassin's and Rhinoceros Auklets at Triangle Island, British Columbia. Condor, **102**: 155–162.

Botsford, L.W., and Lawrence, C.A. 2002. Patterns of co-variability among California Current Chinook salmon, coho salmon, Dungeness crab, and physical oceanographic conditions. Prog. Oceanogr. **53**: 283–305.

Boyd, I.L., and Murray, W.A. 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. J. Anim. Ecol. **70**: 747–760.

Boyd, W.S., Ryder, J.L., Shisko, S.G., and Bertram, D.F. 2000. At-sea foraging distributions of radio-marked Cassin's Auklets breeding at Triangle Island, British Columbia. Canadian Wildlife Service, Pacific and Yukon Region, Delta, B.C. Tech. Rep. Ser. No. 353.

Burger, A.E., and Powell, D.W. 1989. Diving depths and diet of Cassin's Auklet at Reef Island, British Columbia. Can. J. Zool. **68**: 1572–1577.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Springer-Verlag, New York.

Campbell, R.W., Dawe, N.K., McTaggart-Cowan, I., Cooper, J.M., Kaiser, G.W., and McNall, M.C.E. 1990. The birds of British Columbia: Vol. II. University of British Columbia Press, Vancouver, BC.

Carl, G.C., Guiguet, C.J., and Hardy, G.A. 1951. Biology of the Scott Island Group, British Columbia. Report of the Provincial Museum,Victoria, B.C.

Chavez, F.P., Pennington, J.T., Castro, C.G., Ryan, C.G., Michisaki, R.P., Schlining, B., Walz, P., Buck, K.R., McFayden, A., and Collins, C.A. 2002. Biological and chemical consequences of the 1997–1998 El Niño in central California waters. Prog. Oceanogr. **54**: 205–232.

Coyle, K.O., and Pinchuk, A.I. 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. Fish. Oceanogr. **12**: 327–338.

Emslie, S.D., Henderson, R.P., and Ainley, D.G. 1990. Annual variation of primary moult with age and sex in Cassin's Auklet. Auk, **107**: 689–695.

Erikstad, K.E., Fauchakd, P., Tveraa, T., and Steen, H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. Ecology, **79**: 1781–1788.

Freeland, H.J., and Cummins, P.F. 2005. Argo: a new tool for environmental monitoring and assessment of the world's oceans, an example from the N.E. Pacific. Prog. Oceanogr. **64**: 31–44.

Furness, R.W., and Ainley, D.G. 1984. Threats to seabird populations presented by commercial fisheries. *In* Status and conservation of the worlds seabirds. *Edited by* J.P. Croxall, P.G.H. Evans, and R.W. Schreiber. International Council for Bird Preservation (ICBP) Tech. Rep. No. 2. pp. 701-708.

Gaston, A.J. 2003. Synchronous fluctuations of thick-billed murre (*Uria lomvia*) colonies in the eastern Canadian Arctic suggest population regulation in winter. Auk, **120**: 362–370.

Gjerdrum, C., Vallée, A.M.J., Cassady St. Clair, C., Bertram, D.F., Ryder, J.L., and Blackburn, G.W. 2003. Tufted puffin reproduc-

© 2005 NRC Canada

tion reveals ocean climate variability. Proc. Natl. Acad. Sci. U.S.A. **100**: 9377–9382.

Golet, G.H., Irons, D.B., and Estes, J.A. 1998. Survival costs of chick rearing in black-legged kittiwakes. J. Anim. Ecol. **67**: 827–841.

Hare, S.R., Mantua, N.J., and Francis, R.C. 1999. Inverse production regimes: Alaska and west coast Pacific salmon. Fisheries, **24**: 6–14.

Hedd, A., Ryder, J.L., Cowen, L.L., and Bertram, D.F. 2002. Interannual variation in the diet, provisioning and growth of Cassin's Auklet at Triangle Island, British Columbia: responses to variation in ocean climate. Mar. Ecol. Prog. Ser. **229**: 221–232.

Hodum, P.J., Sydeman, W.J., and Visser, G.H. 1998. Energy expenditure and food requirement of Cassin's Auklets provisioning nestlings. Condor, **100**: 546–550.

Jacobson, K.-O., Erikstad, K.E., and Sæther, B.-E. 1995. An experimental study of the costs of reproduction in the kittiwake *Rissa tridactyla*. Ecology, **76**: 1636–1642.

Jones, I.L., Hunter, F.M., and Robertson, G.J. 2002. Annual adult survival of Least Auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. Oecologia, **133**: 38–44.

Kitaysky, A.S., Wingfield, J.C., and Piatt, J.F. 1999. Dynamics of food availability, body condition, and physiological stress response in Black-legged Kittiwakes. Funct. Ecol. **13**: 577–584.

Mackas, D.L., and Galbraith, M. 2002. Zooplankton community composition along the inner portion of Line P during the 1997–1998 El Niño event. Progr. Oceangr. **54**: 423–437.

Mackas, D.L., Thompson, R.E., and Galbraith, M. 2001. Changes in the zooplankton community of the British Columbia continental margin, 1985–1999, and their covariation with oceanographic conditions. Can. J. Fish. Aquat. Sci. **58**: 685–702.

Mackas, D.L., Peterson, W.T., and Zamon, J.E. 2004. Comparisons of interannual biomass of zooplankton communities along the continental margins of British Columbia and Oregon. Deep Sea Res. II, **51**(6–9): 875–896.

Mantua, N. 2000. The Pacific Decadal Oscillation (PDO) [online]. Available from http://tao.atmos.washington.edu/pdo/ [accessed 5 June 2005; updated January 2000].

Mantua, N.J., and Hare, S.R. 2002. The Pacific Decadal Oscillation. J. Oceanogr. **58**: 35–44.

Manuwal, D.A. 1978. Criteria for aging Cassin's Auklets. Bird-Banding, **49**: 157–161.

Manuwal, D.A., and Thoreson, A.C. 1993. Cassin's Auklet (*Ptychoramphus aleuticus*). *In* The birds of North America, no. 50. *Edited by* A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia, Penn, and The American Ornithologists' Union, Washington, D.C.

McGowan, J.A., Cayan, D.R., and Dorman, L.M. 1998. Climate–ocean variability and ecosystem response in the Northeast Pacific. Science (Washington, D.C.), **281**: 210–217.

Nur, N., Sydeman, W.J., Hester, M., and Pyle, P. 1998. Survival in Cassin's Auklets on Southeast Farallon Island: temporal patterns, population viability, and the cost of double brooding. Pac. Seabirds, **25**: 38A. [Abstr.]

Oedekoven, C., Ainley, D.G., and Spear, L.B. 2001. Variable responses of seabirds to change in marine climate: California Current 1985–1994. Mar. Ecol. Prog. Ser. **212**: 265–281.

Peterson, W.T., Keister, J.E., and Feinberg, L.R. 2002. Effects of the 1997–1998 El Niño event on the hydrography and zooplankton of the central Oregon Coast. Prog. Oceanogr. **54**. 381–398.

Pyle, P. 2001. Age at first breeding and natal dispersal in a declining population of Cassin's Auklet. Auk, **118**: 996–1007.

Rodway, M.S. 1991.Status and conservation of breeding seabirds in British Columbia. *In* Seabird status and conservation: a supplement. *Edited by* J.P. Croxall. International Council for Bird Preservation (ICBP) Tech. Publ. No. 11. pp. 43–102.

Rodway, M.S., Lemon, M.J.F., and Summers, K.R. 1990. British Columbia seabird colony inventory: report No. 4 — Scott Islands. Census results form 1982–1989 with reference to the Nestucca oil spill. Canadian Wildlife Service, Pacific and Yukon Region, Delta, B.C. Tech. Rep. Ser. No. 86.

Rodway, M.S., Lemon, M.J.F., and Kaiser, G.W. 1994. British Columbia Seabird Colony inventory: report No.6. Major colonies on the west coast of Graham Island. Canadian Wildlife Service, Pacific and Yukon Region, Delta, B.C. Tech. Rep. Ser. No. 95.

Roemmich, D., and McGowan, J. 1995. Climate warming and the decline of zooplankton in the California Current. Science (Washington, D.C.), **267**:1324–1326.

Ryder, J.L., Boyd, W.S., Shisko, S.G., and Bertram, D.F. 2001. At-sea foraging distributions of radio-marked Cassin's Auklets breeding at Triangle Island, B.C., 2000 Canadian Wildlife Service, Pacific and Yukon Region, Delta, B.C. Tech. Rep. Ser. No. 368.

Sydeman, W.J., and Lee, D.E. 2003. Comparative population biology: oceanographic correlates of seabird survival in the Southern California Current system. Pacific Seabirds, **30**: 64–65. [Abstr.]

Trenbeth, K.E., and Hoar, T.J. 1996. The 1990–1995 El Nino-Southern Oscillation event: Longest on record. Geophys. Res. Lett. **23**: 57–60.

Trudel, M., Zamon, J.E., Trucker, S., and Welch, D.W. 2003. Are salmon starving in the ocean? Can. Tech. Rep. Fish. Aquat. Sci. **2403**: 112–118.

Veit, R.R., Pyle, P., and McGowan, J.A. 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current system. Mar. Ecol. Prog. Ser. **139**:11–18.

Vermeer, K. 1981. The importance of plankton to Cassin's Auklet during breeding. J. Plankton Res. **3**: 315–329.

Ware, D.M., and McFarlane, G.A. 1989. Fisheries production domains in the Northeast Pacific Ocean. *In* Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. *Edited by* R.J. Beamish and G.A. McFarlane. Can. Spec. Publ. Fish. Aquat. Sci. **108**: 359–379.

White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study, **46**(Suppl.): 120–138.

Wolter, K., and Timlin, M.S. 1998. Measuring the strength of ENSO events: How does 1997/1998 rank? Weather, **53**: 315–324.

Appendix A. Validation of eye colour as an index of maturation.

Before subjecting our CMR data to analysis by the computer program MARK (White and Burnham 1999), we tested the veracity of eye colour to index Cassin's Auklet maturation independently for both Triangle and Frederick islands. Specifically we queried if the progression from brown-eyed, through brown–white-eyed (intermediate), to white-eyed was a consistent and reliable index of aging from first-year to second-year and then to older adult birds. We applied two approaches to investigating the relationship between eye colour and age.

In the first approach, we plotted the interannual change in eye colour for that subset of marked birds that were assessed for eye colour in any year t and then again in year $t + 1$ (Fig. A1). We then duplicated this approach for a subset of

© 2005 NRC Canada

Fig. A1. Change in eye colour for individually banded and resighted Cassin's Auklets (*Ptychoramphus aleuticus*) between year t and year $t + 1$ (t = 1994 to 1999) at Triangle and Frederick islands. The change is expressed as the percentage of individuals distributed among three possible eye colour scores in year $t + 1$ conditional on their colour score in year t. Sample sizes in year t are as follows (Triangle Island, Frederick Island): 28, 92 for brown-eyed birds; 207, 132 for brown–white-eyed (intermediate) birds; 1012, 1659 for white-eyed birds.

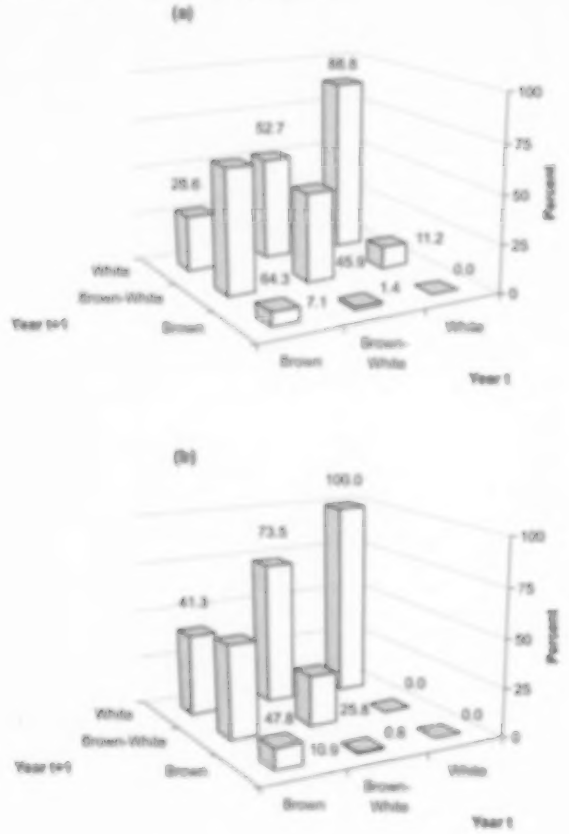
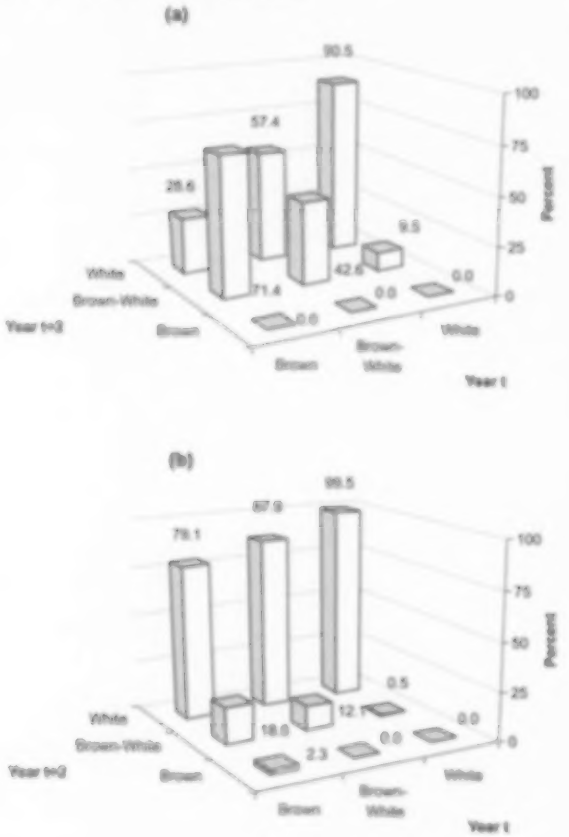


Fig. A2. Change in eye colour for individually banded and resighted Cassin's Auklets (*Ptychoramphus aleuticus*) between year t and year $t + 2$ (t = 1994 to 1998) at Triangle and Frederick islands. The change is expressed as the percentage of individuals distributed among three possible eye colour scores in year $t + 2$ conditional on their colour score in year t. Sample sizes in year t are as follows (Triangle Island, Frederick Island): 7, 43 for brown-eyed birds; 61, 66 for brown–white-eyed (intermediate) birds; 327, 946 for white-eyed birds



marked birds that were assessed for eye colour in any year t and then again in year $t + 2$ (Fig. A2).

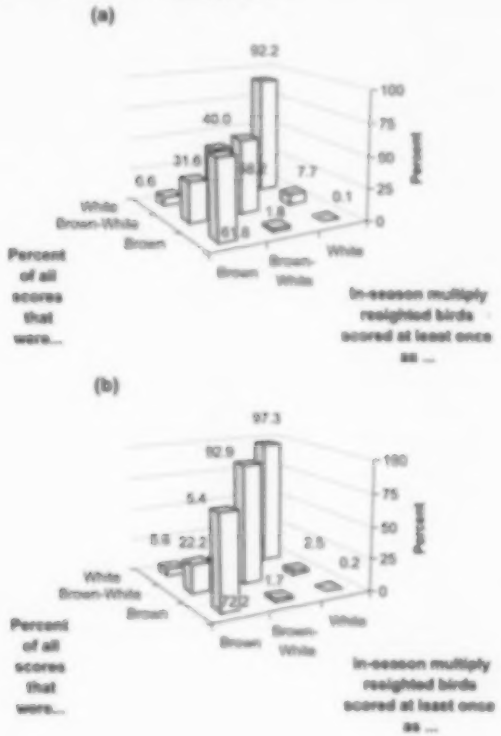
Our second approach assessed the potential for misclassification of eye colour scores. In that approach, we plotted the percent distribution of intraannual eye colour scores for that subset of marked birds that were repeatedly assessed for eye colour within any year t, organized according to each eye colour score observed within the subset (Fig. A3). At Triangle Island, 1286 birds were scored more than once in a year. (At Frederick Island, this number was 293 birds.) About 90% of birds were resighted two or three times within a year, but a few were resighted as many as eight times within a year. Two tacit, yet safe, assumptions of this approach are that eye colour changed insignificantly within the roughly 2-month breeding season and that observers scoring eye type had no memory of previous scores for marked individuals they may have seen earlier in the season.

The interannual change in eye colour portrayed in Figs. A1 and A2 indicates that at both Frederick and Triangle islands, virtually all white-eyed birds remain white-eyed as they age. Though 11.2% and 9.5% of white-eyed birds at Triangle Island were assessed 1 year and 2 years later, respectively, as intermediate (Fig. A1*a*), the intraseasonal evidence of Fig. A3*a* suggests this is probably due to observation error, especially since a retrogression in eye colour from white to intermediate seems statististically unlikely. Note that Fig. A3 demonstrates that scoring of eye colour at Frederick Island was more consistent, in general, than at Triangle Island. The largest inconsistency at Triangle Island occurs among birds scored at least once in a year as brown–white-eyed (intermediate) birds, in that about 40% of the scores for these birds were registered as white.

A less consistent scoring of eye colour at Triangle Island than at Frederick Island is evident also for intermediate-eyed birds in year t that were scored as intermediate 1 and 2 years

© 2005 NRC Canada

Fig. A3. Variation in eye colour scores for in-season, multiply-resighted banded Cassin's Auklets (*Ptychoramphus aleuticus*) within any year t (t = 1994 to 1998) at Triangle and Frederick islands. The change is expressed as the percentage of total scores distributed among three possible eye colour scores conditional on each bird being scored at least once as either brown, brown–white (intermediate), or white in that year. Sample sizes in year t are as follows (Triangle Island, Frederick Island): 76, 18 for brown-eyed birds; 844, 239 for brown–white-eyed (intermediate) birds; 3067, 514 for white-eyed birds.



later (Figs. A1 and A2). At Triangle Island, about 40%–45% of intermediate-eyed birds did not change colour 1 and 2 years later, whereas at Frederick Island only 25.8% and 12.1% of intermediate birds did not change eye colour 1 and 2 years, respectively, later.

Based on the more consistent eye colour scoring at Frederick Island, our data strongly suggest that approximately 2 years are required for most (79.1%; Fig. A2) brown-eyed birds to become white-eyed. The equivalent interpretation for Triangle Island is somewhat equivocal, with only 28.6% of brown-eyed birds being scored as white-eyed 2 years later. Indeed, essentially the same progression of eye colour is observed for those Triangle Island birds scored after only a single year at large. However, if one accepts that the scoring of eye colour on Frederick Island was rigorous, and if one presumes that eye colour progression with age is unlikely to markedly differ between Cassin's Auklet populations, observer inconsistency in scoring eye colour seems the most likely explanation for the lack of eye colour discrimination of age progression (Fig. A3*b*). We are comfortable with this conclusion, since eye colour scoring on Frederick Island was scored by a field crew supervised by one individual who led the CMR program. On Triangle Island, there were both more observers and higher observer turnover during the 7 years of the CMR program there.

Though observation error in scoring eye colour at Triangle Island no doubt contributes to the greater the uncertainty (relative to Frederick Island) in our estimates of survival rates obtained using the computer program MARK for Triangle Island (Table 1), our data are unequivocal that 2 years elapse between the brown-eyed and white-eyed stages for Cassin's Auklets at Frederick and Triangle islands. It follows from this conclusion, and from the support of our data (Figs. A1–A3), that our presumption that each transition from brown-eyed to the intermediate eye colour of brown–white and then to white requires, on average, 1 year.

© 2005 NRC Canada

Effects of seasonal temperature and photoperiod on Atlantic cod (*Gadus morhua*). I. Morphometric parameters and metabolites

H.M. Levesque, C. Short, T.W. Moon, J.S. Ballantyne, and W.R. Driedzic

Abstract: Age-1+ to age-3+ Atlantic cod (*Gadus morhua*) were held at either constant (~9 °C) or ambient ocean temperatures (Newfoundland) from December 2000 to June 2002 under natural photoperiod and ad libitum feeding. Body mass and length, liver total lipids, triacylglycerols and free fatty acids, glycogen and protein from liver and muscle, plasma glucose, and lactate were assessed over this period. Both groups increased body mass, length, and liver mass, with a significantly greater increase for the constant group at all sampling dates. Both groups demonstrated a growth phase from August to October 2001, while the ambient group showed a compensatory growth phase from May to July 2001. Gonad mass significantly increased in males and females from both groups in June 2002. Most tissue metabolites demonstrated seasonal patterns consistent with photoperiod. The effect of temperature was primarily quantitative, implicating temperature changes food conversion efficiencies, as both groups of cod had the same access to food. Under the conditions of this study, Atlantic cod growth is controlled primarily by photoperiod, with temperature affecting the amounts of tissue metabolites.

Résumé : Des morues Atlantiques (*Gadus morhua*) âgées de +1 à +3 années ont été maintenues à la température ambiante de l'océan à Terre-Neuve ou à une température constante (~9 °C) de décembre 2000 jusqu'en juin 2002, sous une photopériode naturelle, et nourries ad libitum. La masse et la longueur du corps, les lipides totaux, les triacylglycérols et les acides gras libres du foie, le glycogène et les protéines musculaires et hépatiques, le glucose et le lactate lasmatiques ont été mesurés à huit reprises pendant la période étudiée. Les deux groupes de poissons ont subi une augmentation de la masse corporelle, de la longueur totale et de la masse du foie durant la période étudiée, avec une augmentation plus grande à toutes les dates d'échantillonnage chez le groupe maintenu à température constante. Il y a une phase de croissance d'août à octobre 2001 chez les deux groupes et une seconde phase de croissance compensatrice de mai 2001 à juillet 2001 chez le groupe maintenu à température ambiante. La masse des gonades des mâles et des femelles a augmenté significativement en juin 2002 chez les deux groupes. La plupart des métabolites tissulaires ont suivi des patrons saisonniers reliés à la photopériode. L'effet de la température est surtout quantitatif et implique des changements des efficacités de conversion de la nourriture, puisque les deux groupes de morues ont un accès identique à la nourriture. Dans les conditions de notre étude, la croissance de la morue atlantique est contrôlée surtout par la photopériode, alors que la température affecte les quantités de métabolites tissulaires.

Introduction

Temperature has a marked effect on growth and developmental rates of teleost fishes (Pelletier et al. 1993; Purchase and Brown 2001; Dutil and Brander 2003), and many fish species, especially in the north temperate regions, demonstrate seasonal patterns of growth and condition in response to temperature changes (Guderley and Gawlicka 1992; Lambert and Dutil 1997). Atlantic cod (*Gadus morhua*) experience natural temperature changes because of geographic location and season (Brander 1995), but little is known about the influence of seasonal temperature changes on Atlantic cod physiology. The decline in Atlantic cod populations has renewed interest in farming this fast-growing and economically important species, and thus the influence of temperature on growth can be of practical interest for aquaculture. Spatial distribution of cod is predominantly controlled by environmental temperature and salinity (Hedger et al. 2004). Cod are, however, widely distributed and can be found in waters that range in temperature from 2 to 11 °C and even higher (Brander 1995; Hedger et al. 2004). Separate cod stocks do exists, each

Received 1 September 2004. Accepted 27 May 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 15 November 2005.
J18293

H.M. Levesque[1] and T.W. Moon. Department of Biology, University of Ottawa, P.O. Box 450, Station A, Ottawa, ON K1N 6N5, Canada.
J.S. Ballantyne. Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada.
C. Short and W.R. Driedzic. Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NL A1C 5S7, Canada.

[1]Corresponding author (e-mail: alevesqu@science.uottawa.ca).

 doi: 10.1139/F05-188 © 2005 NRC Canada

with somewhat different preferred thermal optima (Hedger et al. 2004), but temperature is considered a key factor in stock production (Brander 1995).

Many studies of cold adaptation report morphometric changes, including a proportional increase in organ size. For example, Kent et al. (1988) reported an increase in hepatosomatic index (HSI) in channel catfish (*Ictalurus punctatus*) acclimated at 15 °C compared with 25 °C, and Blier and Guderley (1988) similarly found an increase in HSI in lake whitefish (*Coregonus clupeaformis*) acclimated to cold temperature (4 °C). Changes in energy reserves may also occur, including increases in blood glucose and liver and muscle metabolites (Martinez et al. 1999; Purchase and Brown 2001; Hochachka and Somero 2002). Modifications of lipids resulted in the increased incorporation of unsaturated fatty acids into membrane phospholipids to maintain optimal membrane fluidity at lower temperatures (Seddon and Prosser 1997). Liver lipids are also the first energetic reserves to be metabolized by fish (Black and Love 1986; Kirsch et al. 1998) and are an important source of essential nutrients (Mishra and Samantaray 2004). Seasonal changes also affect prey availability and prey diversity, which may influence lipid composition of fish liver and muscle (Kirsch et al. 1998), as well as other tissue metabolites. Temperature also affects protein synthesis and RNA and DNA levels in juvenile cod (Foster et al. 1992), with higher amino acid incorporation at 15 °C than at 5 °C (Foster et al. 1992).

Seasonal changes in morphometrics and biochemistry may reflect more than simply temperature because of the co-occurrence of dietary and photoperiod changes. Several studies report that muscle and liver metabolic organization varies seasonally, independent of temperature changes (Kleckner and Sidell 1985; Seddon and Prosser 1997). Photoperiod regulation of seasonal changes in physiology is a well-known phenomenon in vertebrates (McCormick et al. 2000). Isolating and identifying the roles of photoperiod versus temperature on various adaptive characteristics of cod can be used to develop improved methods for enhancing growth under aquaculture conditions.

For this reason, we conducted a long-term study to investigate the morphometric and biochemical changes of age-1+ to age-3+ Atlantic cod with high food availability as would occur in an aquaculture situation. Fish were held either at ambient ocean temperatures (ABT) (area of St. John's, Newfoundland) or at constant temperature (CST; 9 °C) over an 18-month period. The CST of 9 °C was chosen based on the preferred thermal range of Newfoundland cod stocks (Purchase and Brown 2001), the relationship between cod growth and temperature (Brander 1995), and the fact that 9 °C is an intermediate water temperature found in waters used within the cod holding facility during the summer (see Fig. 1); this temperature is within the lower growth temperature range for cod (Pedersen and Jobling 1989; Pelletier et al. 1993). Fish were sampled at regular intervals over this period, and a variety of morphometric and biochemical parameters were determined. A second part of this study (Levesque et al. 2005) examines enzyme changes that accompany these growth and tissue metabolite changes. The aims of this study are to determine the temperature and season of cod's greatest growth and if seasons influence metabolite storage in Atlantic cod.

Materials and methods

Experimental animals and procedures

Atlantic cod hatched in March 1999 from stocks caught in Gooseberry Cove, Newfoundland (Northwest Atlantic Fisheries Organization (NAFO) region 3L; 48°N, 53°W), were maintained at the Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. Fish were divided into two groups in October 2000 and kept in seawater tanks under natural photoperiod. In late November 2000, one group was placed under natural ocean water temperatures and a second group was held at a CST of –9 °C. Each tank was 5 m in diameter and 1.2 m in height, containing approximately 20 000 L of seawater; cod density was approximately 2 g fish·L^{-1} throughout the sampling period. The temperature and photoperiod changes experienced by both groups are presented (Fig. 1). Both groups were fed twice daily to satiation on a commercial pellet feed (Shur-Gain, Truro, Nova Scotia: 45.0% protein; 22.0% fat; 4.0% fibre; 1.6% calcium; 1.2% phosphorus; 0.7% sodium; 10 000 IU·kg^{-1} vitamin A; 4000 IU·kg^{-1} vitamin D; 250 IU·kg^{-1} vitamin E). Every 2–3 months, 10 cod from each group were sacrificed by a blow to the head. Length and mass were recorded for each fish. Blood was collected from the caudal vessels into a heparinized syringe and centrifuged at 12 000*g* for 3 min. The resulting plasma was frozen in liquid nitrogen and stored at –80 °C until used. Liver and gonad masses were recorded, and samples of hypaxial white muscle (at the dorsal fin level) and liver were immediately frozen in liquid nitrogen and stored at –80 °C. Condition factor ((body mass (g) / length (cm^3)) × 100), somatic indices for gonad and liver ((organ mass (g) / body mass (g)) × 100), and growth rate (% body mass·day^{-1}) ((ln (mass *b*) – ln (mass *a*)) / (time *b* – time *a*)) were calculated.

Biochemical analyses

Glycogen analysis

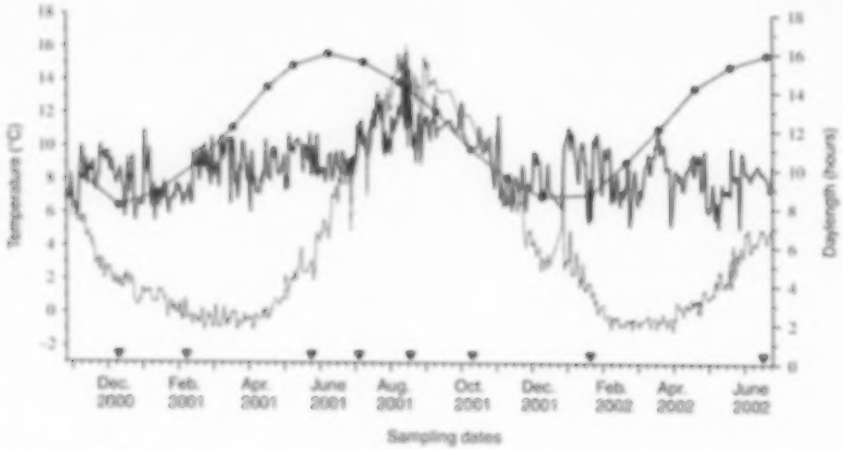
Liver and muscle glycogen were determined as glucose equivalents after amyloglucosidase hydrolysis of the sample and after measuring the difference in glucose content before and after hydrolysis, according to Keppler and Decker (1974). Briefly, frozen pieces of tissue were homogenized by a 4 s burst from a cell ultrasonic disrupter (Kontes, Mandel Scientific Ltd., Montreal, Quebec) in 3 vol of 6% perchloric acid, followed by centrifugation at 10 000*g* for 5 min. After the addition of 0.5 vol of 2 mol·L^{-1} $NaHCO_3$, supernatants were digested with amyloglucosidase in acetate buffer (pH 4.8) for 2 h at 37 °C with constant agitation. The reaction was stopped by the addition of 25 µL 70% perchloric acid followed by centrifugation at 7000*g* for 10 min. Supernatants were used for glucose analysis (see below).

Liver lipid analysis

Lipids were extracted in chloroform–methanol using a Folch procedure (Folch et al. 1957) modified according to Parrish (1998). Lipid classes were separated using a MARK V Iatroscan (Iatroscan Laboratory, Tokyo, Japan) analyzer as described by Parrish (1987). Extracts were spotted onto silica-gel-coated chromarods, and a three-stage development system was used. Fatty acid composition of the extracted lipids was estimated from fatty acid methyl esters (FAMEs),

© 2005 NRC Canada

Fig. 1. Temperature and photoperiod profiles (sampling dates denoted by an arrowhead) of Atlantic cod (*Gadus morhua*) held under constant (9 °C) (solid line) or ambient (dotted line) seawater temperatures from November 2000 to June 2002. Solid circles represent photoperiod.



which were prepared using 10% boron trifluoride in methanol and heating to 100 °C for 1 h (Morrison and Smith 1964; Budge 1999). FAMEs were separated by gas chromatography (Varian model 3400 GC equipped with a Varian 8100 autosampler; Varian Inc., Palo Alto, California) using an Omegawax 320 column (Supelco, Bellefonte, Penn.). For more details on lipid class separation and fatty acid analyses, see Copeman et al. (2002).

Plasma lactate and glucose

Plasma lactate and glucose were measured enzymatically using lactate dehydrogenase and hexokinase plus glucose-6-phosphate dehydrogenase, respectively, by following the appearance of NADH at 340 nm using a microplate reader (SpectraMax Plus 384; Molecular Devices, Sunnyvale, California) and values calculated from standard curves using Soft Max Pro.

Statistics

Results are presented as means ± standard error. Statistical analyses were performed using SPSS (version 12.0, SPSS Inc., Chicago, Illinois) and SYSTAT (version 10, Systat Software Inc., Point Richmond, California). One-way analyses of variance (ANOVA) were performed at each time point, with a Bonferroni-adjusted critical value (α) of 0.00625. Two separate one-way ANOVAs were performed on each treatment. When the one-way ANOVA showed significant effects, multiple mean comparisons were made using the Tukey–Kramer comparison. A Pearson's correlation was performed on SYSTAT results.

Results

Physical condition of the fish

Atlantic cod at all temperatures continued to eat and remained active throughout the entire experimental period. The initial mass, length, and condition factor of the cod at the first sampling date did not differ between groups (Figs. 2*a*, 2*b*, 2*c*). Body mass and length increased for both groups from December 2000 to June 2002, with a significantly ($p < 0.01$) greater increase for fish held at CST compared with ABT (Fig. 2*a*, 2*b*). Both CST and ABT fish exhibited a significant increase in mass between the August 2001 and October 2001 sampling times. The ABT fish exhibited a significant increase in growth between May 2001 and July 2001 that was not observed in the CST fish (Figs. 2*a*, 2*b*). Condition factor remained unchanged between groups and across the entire period of the study, except for the CST group in October 2000, where condition factor was significantly elevated (Fig. 2*c*).

Liver mass and HSI followed the same trend in both groups (Figs. 3*a*, 3*b*). HSI followed an annual cycle that was opposite to that of photoperiod (cf. Fig. 3*b* with Fig. 1). Liver mass was significantly greater in the CST group from May 2001 to January 2002, whereas the HSI was not significantly different between groups except in June 2002, where it was higher in the ABT group (Figs. 3*a*, 3*b*). Liver mass exhibited a significant increase in both groups between August 2002 and October 2002. Liver mass per body length followed a pattern identical to that of the HSI (data not shown).

Age-3+ individuals were reproductively mature in June 2002, as evidenced by the increased gonad somatic index (GSI) for both females and males (Figs. 4*b*, 4*c*). GSI was different between groups only in June 2002, with GSI for the CST group 2-fold higher for females and 1.5-fold higher for males compared with the ABT group (Figs. 4*a*, 4*b*). The pattern of variation in gonad mass was not different from that of the GSI (data not shown).

Liver lipids

Total lipids and triacylglycerols (TAG) per gram of liver did not differ between the CST and the ABT groups, except in May 2001 when the CST group was significantly higher than the ABT group (Figs. 5*a*, 5*b*). In the ABT group, both total lipids per gram and TAG per gram followed the same trend as liver mass, decreasing from December 2000 to May 2001, followed by an increase to January 2002. The CST

© 2005 NRC Canada

Fig. 2. Body morphometric parameters of Atlantic cod (*Gadus morhua*) throughout the 18-month sampling period (○, constant temperature (9 °C) cod; ●, ambient temperature cod; sampling dates denoted by an arrowhead). Condition factor is expressed by (body mass (g)-length $(cm^3)^{-1}$) × 100 in panel *c*. Each point represents the mean ± standard error of $n = 10$. An asterisk (*) indicates values significantly ($p < 0.01$) different between groups at the same time point. Letters that are different represent significant differences between sampling months within the same group; uppercase letters indicate differences within the constant temperature group, and lowercase letters indicate differences within the ambient temperature group. Numbers on each line represent the rate of change in specific growth rate between the two time points.

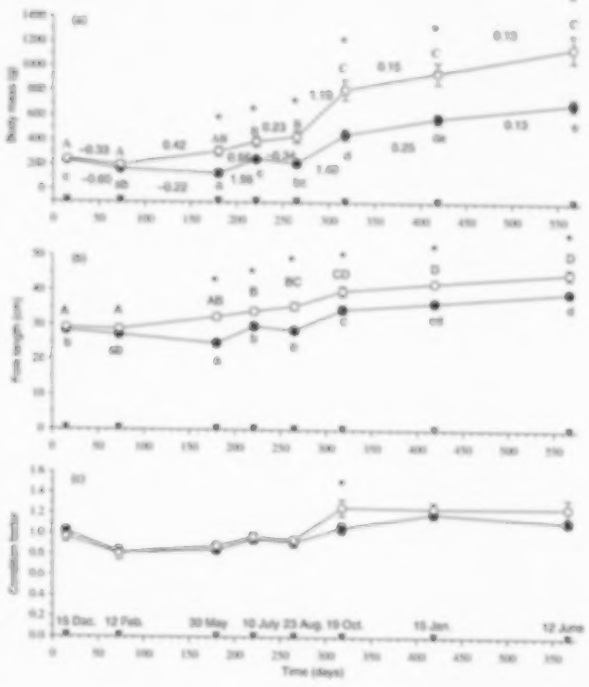
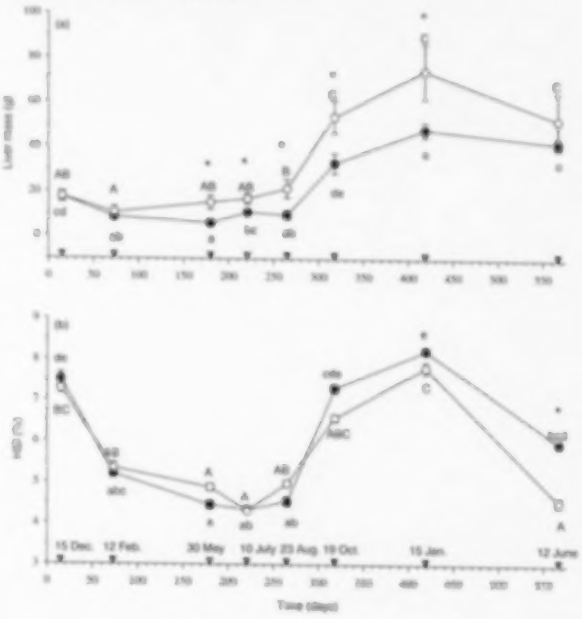


Fig. 3. Changes in hepatic parameters of Atlantic cod (*Gadus morhua*) throughout the 18-month sampling period (○, constant temperature (9 °C) cod; ●, ambient temperature cod; sampling dates denoted by an arrowhead). Hepatosomatic index (HSI) is expressed by (liver mass (g)-body mass $(g)^{-1}$) × 100 in panel *b*. Each point represents mean ± standard error, $n = 10$. An asterisk (*) indicates values significantly different between groups at the same time point. Letters that are different represent significant differences between sampling months within the same group; uppercase letters indicate differences within the constant temperature group, and lowercase letters indicate differences within the ambient temperature group.



group showed no significant change in lipid content ($mg \cdot g^{-1}$ liver) over the entire 18-month period. TAG content was more variable and followed a pattern similar to that of total lipids in the CST group. Total liver lipids per body mass or body length (data not shown) followed the same pattern as total liver lipids per gram of liver.

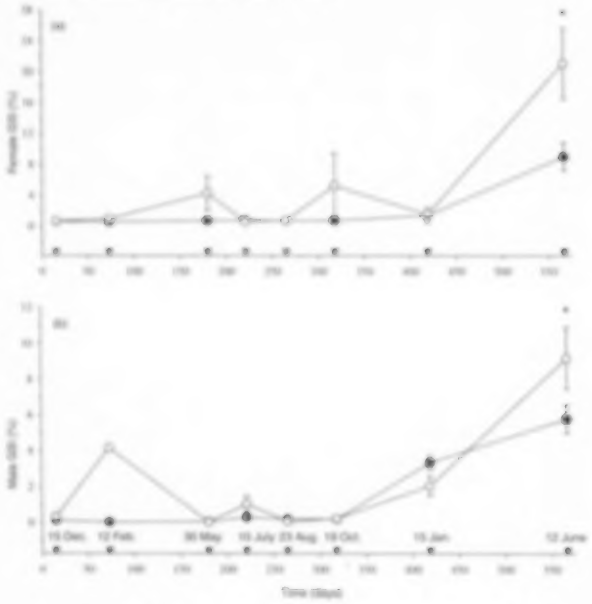
The percent composition of selected liver fatty acids is provided (Tables 1 and 2). Liver fatty acids were further characterized as saturated, monounsaturated, polyunsaturated, omega-3 and omega-6. For both groups, 16:0, 18:1ω9, and 22:6ω3 were the most abundant saturated fatty acids, and fatty acid composition from the ABT and CST groups followed the same trends. Liver omega-3 fatty acids and the sum of the polyunsaturated fatty acids (PUFA) were correlated ($r^2 = 0.91$, $p < 0.001$) and increased with age and mass of the fish in both groups. PUFA and omega-3 were correlated with the mass of the fish ($r^2 = 0.68$, $p < 0.001$, and $r^2 = 0.70$, $p < 0.01$, respectively), and omega-3 was correlated with fish liver mass ($r^2 = 0.69$, $p < 0.01$). The sum of the monounsaturated fatty acids (MUFA) and the sum of the omega-6 fatty acids were the highest in May 2001 for both groups. MUFA and omega-6 were negatively correlated ($r^2 = -0.57$, $p < 0.001$). MUFA was also negatively correlated with PUFA ($r^2 = -0.71$, $p < 0.001$) and fish mass ($r^2 = -0.65$, $p < 0.001$). Omega-6 was negatively correlated with fish liver mass ($r^2 = -0.56$, $p < 0.001$). The sum of the saturated fatty acids in the ABT group was higher from July 2001 to January 2002, whereas the sum of the unsaturated fatty acids was the highest in June 2002. There were very few differences in liver fatty acid composition between CST and AST groups.

Plasma and liver carbohydrate and liver and muscle protein

Plasma glucose of the CST group was higher in December 2000 and February 2001 and lower in August 2001 compared with the ABT group (Fig. 6*a*). Plasma lactate followed the same pattern in both groups, with the highest levels in May 2001 (Fig. 6*b*). Plasma lactate was higher from December 2000 to May 2001 in the CST group (Fig. 6*b*). Plasma glucose was lowest and plasma lactate was highest in May

© 2005 NRC Canada

Fig. 4. Changes in the gonad somatic index (GSI = (gonad mass (g)·body mass $(g)^{-1}$) × 100) of Atlantic cod (*Gadus morhua*) throughout the 18-month sampling period for (*a*) females and (*b*) males (○, constant temperature (9 °C) cod; ●, ambient temperature cod; sampling dates denoted by an arrowhead). $n = 5$ in June 2002; for all other dates, $1 \leq n \leq 9$ because of random sampling. Each point represents mean ± standard error when $n > 2$. An asterisk (*) indicates values significantly different between groups at the same time point. Letters that are different represent significant differences between sampling months within the same group; uppercase letters indicate differences within the constant temperature group, and lowercase letters indicate differences within the ambient temperature group.



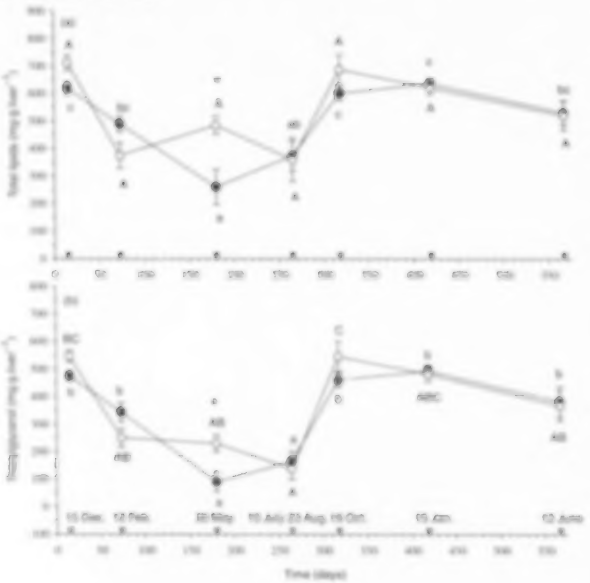
for both groups, suggesting an enhanced anaerobic metabolism at this time.

Total liver glycogen was the highest in October 2001 and January 2002 and declined significantly in the CST cod in June (Fig. 7*a*). There were no differences between the CST and ABT group across the period studied. Muscle glycogen was significantly higher in the CST group in May 2001 and June 2002 (Fig. 7*b*). There was more than a twofold increase in muscle glycogen between May 2001 and July 2001 in both groups. Liver glycogen was positively correlated with HSI ($r^2 = 0.62$, $p < 0.001$).

Total liver glycogen was the highest in October 2001 and January 2002. There were no differences between the CST and ABT groups (Fig. 7*a*). Muscle glycogen was significantly higher in the CST group in May 2001 and June 2002 (Fig. 7*b*). There was more than a twofold increase in muscle glycogen between May 2001 and July 2001. Liver glycogen was correlated with HSI ($r^2 = 0.62$, $p < 0.001$).

Total liver protein was also higher in October 2001 and January 2002 (Fig. 8*a*). Total liver protein was highly correlated with total liver glycogen ($r^2 = 0.73$, $p < 0.001$), fish mass ($r^2 = 0.78$, $p < 0.001$) and length ($r^2 = 0.76$, $p < 0.001$), and HSI ($r^2 = 0.58$, $p < 0.001$). Muscle protein (Fig. 8*b*) was

Fig. 5. Changes in (*a*) total liver lipids and (*b*) triacylglycerol in Atlantic cod (*Gadus morhua*) throughout the 18-month sampling period (○, constant temperature (9 °C) cod; ●, ambient temperature cod; sampling dates denoted by an arrowhead). Each point represents mean ± standard error, $n = 5$. An asterisk (*) indicates values significantly different between groups at the same time point. Letters that are different represent significant differences between sampling months within the same group; uppercase letters indicate differences within the constant temperature group, and lowercase letters indicate differences within the ambient temperature group.



similar between thermal groups (except at the beginning of the experiment), with changes occurring in a cyclic manner. One interesting point is that a sharp, significant decrease in muscle protein between August 28 and October 19 is associated with a period of the most rapid body mass increase (cf. Fig. 8*b* with Fig. 2).

Discussion

The present study was conducted to gather basic data on the effect of fluctuating environmental temperature relative to constant temperature on Atlantic cod morphometry and physiology. These studies were undertaken in juvenile cod fed ad libitum as would occur in an aquaculture facility. By understanding changes in body parameters, we should be able to establish the impact of temperature and season on cod metabolism and especially growth.

Body mass and length significantly increased for both groups during the experiment, with a significantly higher growth for the CST group compared with the ABT group. Overall body mass from the beginning to end of the experiment increased 2.8- and 4.5-fold, respectively, for the ABT and CST cod, showing that temperature does impact body mass gain over the year. Pedersen and Jobling (1989) previously reported that low temperatures depressed Atlantic cod growth. In our study, food was not limited, and body mass

© 2005 NRC Canada

Table 1. Percent composition of selected fatty acids in the liver of Atlantic cod (*Gadus morhua*) (n = 5) held at ambient temperature.

	Liver lipid level (%)						
Fatty acid	6 Dec. 2000	12 Feb. 2001	30 May 2001	10 July 2001	19 Oct. 2001	15 Jan. 2002	10 June 2002
14:0	3.63±0.24	3.66±0.28	3.75±0.67	4.47±0.49	3.86±0.23	4.18±0.22	3.90±0.45
16:0	13.61±0.50	13.23±0.96	13.39±0.48	14.78±1.81	13.76±0.66	13.56±0.49	11.91±1.06
16:1ω7	6.38±0.41	7.19±0.44	7.93±0.83	8.15±0.82	6.75±0.36	6.58±0.30	6.02±0.13
18:0	3.13±0.30	2.91±0.70	3.11±0.49	3.67±0.57	3.06±0.30	3.27±0.26	2.91±0.44
18:1ω9	20.75±0.50	21.23±1.29	21.77±2.18	14.79±9.92	20.50±0.67	18.42±1.61	17.05±1.65
18:1ω7	4.07±0.23	4.30±0.31	4.58±0.50	4.12±0.22	3.82±0.53	4.01±0.35	3.70±0.36
18:2ω6	6.04±0.55	8.38±2.02	9.43±1.48	9.06±0.93	5.80±0.67	5.24±0.45	4.71±0.38
20:1ω9	6.30±1.37	6.99±0.65	6.91±1.54	5.45±0.30	4.84±0.32	5.81±0.60	7.37±0.69
20:4ω6	0.65±0.05	0.58±0.06	0.51±0.15	0.73±0.14	0.66±0.05	0.61±0.05	0.57±0.05
20:5ω3	9.09±1.26	6.60±0.93	6.25±2.31	10.15±1.99	10.02±0.79	9.56±0.83	8.27±1.10
22:1ω11	3.98±1.17	4.87±1.02	4.60±1.61	3.14±0.15	3.01±0.58	3.69±0.29	4.48±0.77
22:6ω3	11.72±1.26	9.31±1.87	7.12±1.90	9.29±1.70	12.53±0.80	13.92±0.78	17.30±1.85
Sum PUFA*	36.23±2.58abc	33.49±2.37bc	31.86±3.98c	39.35±5.82ab	38.45±1.11ab	38.72±1.77ab	40.64±1.40a
Sum MUFA*	42.08±2.37ab	45.50±1.66a	46.58±3.99a	36.35±8.87b	39.47±0.80ab	39.05±1.84ab	39.23±1.08ab
Sum ω3*	26.85±2.89abc	21.40±3.28cd	18.58±4.31d	25.45±4.39bc	29.02±1.15ab	30.15±2.05ab	32.721±0.04a
Sum ω6*	7.27±0.52b	9.77±2.04a	10.69±1.41a	10.65±1.16b	7.03±0.71b	6.38±0.43b	5.92±0.50a
Sum unsaturated*	78.31±0.59a	78.99±1.33a	78.44±0.59ab	75.70±3.10b	77.93±0.76ab	77.77±0.37ab	79.87±1.02a
Sum saturated*	21.69±0.59ab	21.01±1.33b	21.55±0.58ab	24.30±3.10a	22.07±0.76ab	22.23±0.37ab	20.13±1.02b

Note: Only the most abundant fatty acids are reported. PUFA, polyunsaturated fatty acids; MUFA, monounsaturated fatty acids; ω3, omega-3 fatty acids; ω6, omega-6 fatty acids. Letters that are different represent significant ($p < 0.01$) differences between sampling month within the same group.
*Calculations were made using additional fatty acids that occurred at lower levels.

Table 2. Percent composition of the content of selected fatty acids in the liver of Atlantic cod (*Gadus morhua*) (n = 5) held at constant temperature (9 °C).

	Liver lipid level (%)						
Fatty acids	6 Dec. 2000	12 Feb. 2001	30 May 2001	10 July 2001	19 Oct. 2001	15 Jan. 2002	10 June 2002
14:0	3.99±0.28	3.84±0.49	4.16±0.89	3.70±0.31	3.85±0.07	3.57±0.36	3.80±0.15
16:0	13.72±0.47	12.63±0.73	12.01±0.86	13.06±0.61	14.78±0.69	12.94±0.41	12.36±0.14
16:1ω7	6.79±0.42	7.35±0.70	8.41±1.12	7.83±0.46	6.51±0.28	6.61±0.42	7.09±0.14
18:0	3.00±0.31	2.30±0.41	1.89±0.55	2.63±0.18	3.22±0.40	3.44±0.43	2.55±0.16
18:1ω9	20.15±0.68	20.46±0.99	20.76±2.47	21.86±0.86	20.85±0.46	19.94±1.45	29.46±0.59
18:1ω7	4.09±0.33	3.97±0.08	3.88±0.29	4.06±0.36	3.79±0.38	4.04±0.42	3.93±0.16
18:2ω6	6.41±0.65	7.08±0.87	9.15±2.83	8.05±0.70	5.67±0.40	4.86±0.51	5.02±0.33
20:1ω9	6.97±0.46	6.97±0.46	8.18±0.88	6.41±0.53	5.64±0.17	5.06±0.32	6.29±0.28
20:4ω6	0.64±0.03	0.63±0.03	0.71±0.13	0.67±0.04	0.60±0.03	0.72±0.03	0.65±0.02
20:5ω3	8.63±0.52	7.64±0.36	6.27±0.55	8.54±1.05	8.64±0.64	10.65±0.67	9.35±0.27
22:1ω11	4.55±0.52	4.56±0.52	5.78±1.06	3.90±0.41	3.81±0.38	2.81±0.41	3.89±0.27
22:6ω3	10.82±0.63	10.86±0.94	8.38±2.82	8.63±0.92	12.04±1.01	13.53±0.35	14.24±0.55
Sum PUFA*	34.88±0.94c	35.38±1.78bc†	32.59±0.56c	34.71±2.05c	35.46±2.10bc†	39.68±1.70a	38.66±1.75ab
Sum MUFA*	43.14±0.63bc	44.46±1.35b	48.05±0.68a	44.77±1.81b	41.17±1.05cd†	39.01±1.33d	41.19±1.36cd†
Sum ω3*	25.32±0.86cd	24.91±1.18cd	19.66±3.26e	22.94±2.02de	26.76±1.91bc	30.94±1.03a	30.29±1.41ab†
Sum ω6*	7.57±0.64bc	8.43±1.00abc	10.64±2.92a	9.45±0.67ab	6.80±0.47c	6.22±0.49c	6.31±0.77c
Sum unsaturated*	78.02±0.45cd	79.85±1.04ab†	80.65±0.61a	79.48±0.58ab†	76.63±1.10d	78.69±0.57bc†	79.85±0.51ab
Sum saturated*	21.98±0.45ab	20.15±1.04cd†	19.29±0.66d	20.52±0.58cd†	23.37±1.10a	21.31±0.57bc†	20.15±0.51cd

Note: Only the most abundant fatty acids are reported. PUFA, polyunsaturated fatty acids; MUFA, monounsaturated fatty acids; ω3, omega-3 fatty acids; ω6, omega-6 fatty acids. Letters that are different represent significant ($p < 0.01$) differences between sampling month within the same group.
*Calculations were made using additional fatty acids that occurred at lower levels.
†Values significantly different between groups at the same time point.

and length increased linearly from February 2001 for the CST group and from May 2001 for the ABT group until the end of the experiment. The significantly higher specific growth rate between August and October 2001 for both groups (1.19% body mass·day^{-1} for CST and 1.40% body mass·day^{-1} for ABT group) must be considered as the period of the year dedicated to accelerated somatic growth for Atlantic cod. What is interesting is that this rapid growth period is associated with a decrease in muscle protein, supporting the idea that mass gain may be initially a result of water content change that is only later replaced by tissue carbon (Mommsen 1998). In fact, muscle protein does not return to

© 2005 NRC Canada

Fig. 6. Plasma (*a*) glucose and (*b*) lactate concentrations in Atlantic cod (*Gadus morhua*) throughout the 18-month sampling period (○, constant temperature (9 °C) cod; ●, ambient temperature cod; sampling dates denoted by an arrowhead). Each point represents mean ± standard error, $n = 10$. An asterisk (*) indicates values significantly different between groups at the same time point. Letters that are different represent significant differences between sampling months within the same group; uppercase letters indicate differences within the constant temperature group, and lowercase letters indicate differences within the ambient temperature group.

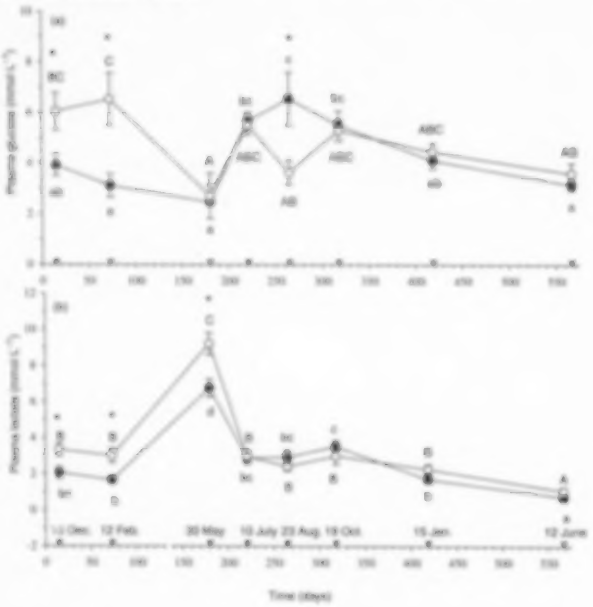
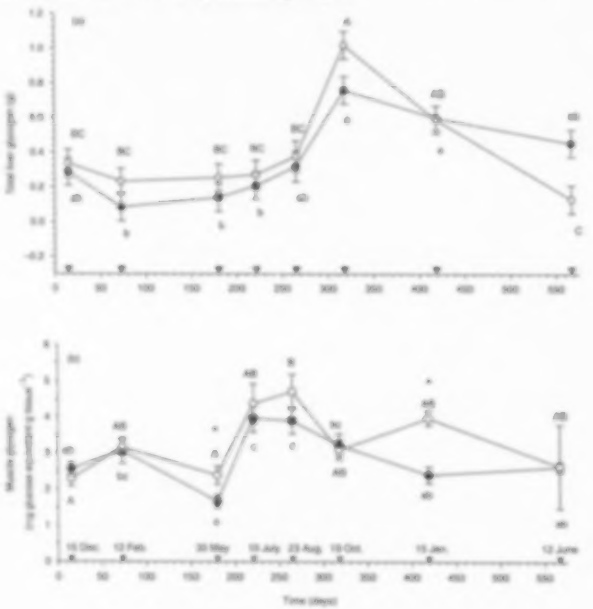


Fig. 7. (*a*) Total liver glycogen and (*b*) muscle glycogen concentrations in Atlantic cod (*Gadus morhua*) throughout the 18-month sampling period (○, constant temperature (9 °C) cod; ●, ambient temperature cod; sampling dates denoted by an arrowhead). Each point represents mean ± standard error, $n = 10$. An asterisk (*) indicates values significantly different between groups at the same time point. Letters that are different represent significant differences between sampling months within the same group; uppercase letters indicate differences within the constant temperature group, and lowercase letters indicate differences within the ambient temperature group.

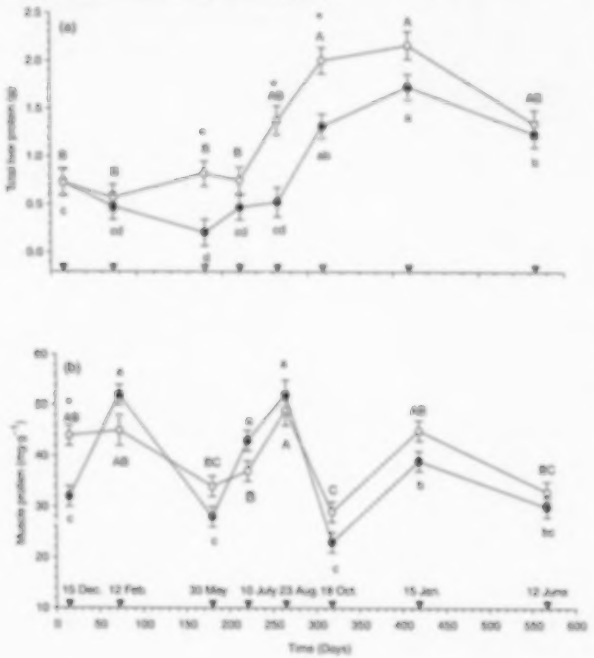


prior growth levels until January 2002 (Fig. 8*b*). At this time, cod are not sexually maturing, so energy can be directed specifically to somatic rather than gonadal growth. This mass gain also occurs at a time when cod are preparing for winter, when photoperiod and temperature are declining. Photoperiod was identical for both groups in this experiment, which may explain why both the CST and ABT groups exhibited a higher growth rate prior to winter, implying that mass gain may be affected by photoperiod. The ABT group also exhibited a higher specific growth rate between May and July 2001 (1.56% body mass·day^{-1}). This period coincides with the time of the year when ocean temperatures change rapidly (from nearly 0 to 9 °C). This accelerated growth noted for the ABT group may represent compensatory growth following the low temperature winter period. Compensatory growth is described as exceptionally fast growth that occurs following a slow growth period caused by reduced feeding (Bélanger et al. 2002). It has been shown that Atlantic cod tend to restore their energy reserves after a period of food restriction (Black and Love 1986; Guderley et al. 2001). In our experiment, the low temperatures experienced by the ABT cod in winter probably depressed appetite, thus inducing compensatory growth in the spring. Presumably, appetite remained constant in the CST group, while it increased in the ABT group, as temperatures rose so that only the ABT group exhibited a second period of accelerated growth during the year. Guderley et al. (2001) showed that food intake increases in the stickleback as temperatures rise.

Liver mass and HSI showed the same cyclic pattern for both groups, but liver mass was consistently higher in the CST group compared with the ABT group, consistent with the higher body mass of CST group. This pattern of a higher liver mass and HSI in the fall and early winter followed by lower values in spring and summer was also reported by Lambert and Dutil (1997) in their study of the St. Lawrence Atlantic cod. Increased liver mass at cold temperatures has been reported in lake whitefish (Blier and Guderley 1988) and channel catfish (Kent et al. 1988). The current work with Atlantic cod indicates that metabolic reserves are accumulated in the liver coincident with the maximum growth period, and then these reserves are mobilized as needed during the winter. In our study, both groups experienced the same pattern of HSI variation, supporting the premise that changes in HSI are driven more by photoperiod than by temperature and metabolic demand. Cod liver stores considerable energy during the feeding period (Black and Love 1986) and uses these hepatic reserves during starvation periods, thus reducing the need to mobilize proteins (and thereby enzyme activity) from skeletal muscle (Martinez et

© 2005 NRC Canada

Fig. 8. (*a*) Total liver protein and (*b*) muscle protein content concentrations in Atlantic cod (*Gadus morhua*) throughout the 18-month sampling period (○, constant temperature (9 °C) cod; ●, ambient temperature cod; sampling dates denoted by an arrowhead). Each point represents mean ± standard error, $n = 10$. An asterisk (*) indicates values significantly different between groups at the same time point. Letters that are different represent significant differences between sampling months within the same group; uppercase letters indicate differences within the constant temperature group, and lowercase letters indicate differences within the ambient temperature group.



al. 1999). Lipid accumulation is typical of growing cod (Black and Love 1986) and leads to high values of HSI.

GSI increased in June 2002 in both groups, but the increase was higher in the CST than in the ABT group. Photoperiod is a more important factor than temperature for sexual maturation, as reported by Johnston et al. (2003) in Atlantic salmon (*Salmo salar*). In our study, Atlantic cod initiated sexual maturation in June 2002 as age-3+ fish. Godø and Haug (1999) reported that growth rate is correlated with cod sexual maturity and that rapidly growing individuals will attain maturity at a younger age and at a shorter length than slow-growing and late-maturing individuals.

It is well established that fatty acid composition of a diet influences the lipid composition of tissues such as liver and muscle (Dos Santos et al. 1993; Kirsch et al. 1998). It is also known that temperature affects both digestion and utilization of food and growth (Shcherbina and Kazalauskene 1971). Liver is the primary site of lipid deposition and storage in fish. Adult wild cod feed on various prey items including a wide variety of fish species, as well as various invertebrates (Lilly 1991). In the wild, the prey available for cod changes with seasons, whereas in our experiment, diet quantity and quality remained the same and abundant over the entire study period. The differences between groups and seasons can be attributed to the temperature. Cod fatty acids and lipids are also important metabolites to look at, as they are the precursor of many hormones; in this context, both lipid quality and quantity are important for fish growth and development (Mishra and Samantaray 2004). In our study, total lipids and TAG per gram liver followed the same pattern as liver mass and HSI, suggesting fat accumulation contributes to changes in liver mass. In contrast with mammals, where adipose tissue is the main site of lipid storage, many fish species use the liver and skeletal muscle (i.e., red muscle) for lipid storage (Jobling 1988). Enlarged livers develop in cultured gadoid fish (Nanton et al. 2003), in part because of diet and lifestyle of these species, and this is especially problematic in aquacultured Atlantic cod (Grant et al. 1998). Liver TAGs and total lipids had roughly identical values. TAGs are the storage form of lipids and a key energy source for locomotion and reproduction in fish. The fatty acid composition of the liver of cod found in our study is close to the composition reported in another cod study by Dos Santos et al. (1993) and the composition of juvenile haddock liver (Nanton et al. 2003). However, there were very few differences between the CST and ABT groups or the sampling periods in our study, supporting previous reports that diet lipid composition and possibly age are the main factors determining fatty acid composition in Atlantic cod liver (Dos Santos et al. 1993; Shahidi and Dunajski 1994; Nanton et al. 2003). The increase in the sum of the PUFA and omega-6 fatty acids also indicates that these fatty acids accumulate in the body with age and, presumably, with reproductive activity as suggested by Henderson and Tocher (1987).

Plasma glucose in the ABT cod followed an annual cycle comparable to that of liver mass, HSI, and total lipids, except it is shifted to the left, with the highest plasma glucose values in August 2001. The CST group showed no trend, although values were significantly higher than the ABT fish between December 2000 and February 2001. These higher plasma glucose values may indicate the CST cod were stressed at this early period, as plasma glucose levels generally rise with stress in fish (Wendelaar Bonga 1997). Plasma lactate showed the same trend in both groups, with the highest values noted in May 2001. It is interesting to note that plasma lactate is highest when plasma glucose values are the lowest in both groups in May 2001, when ambient photoperiod and temperature are increasing. These data support those of Mayerle and Butler (1971), which showed blood glucose decreased as blood lactate increased in the American eel (*Anguilla rostrata*) as water temperature rose. Atlantic cod liver glycogen in our study varied in an unpredictable manner, as reported by Seddon and Prosser (1997) in channel catfish. It is important to note, however, that in the ABT group, liver glycogen is higher from May 2001 to June 2002, which could be explained by a compensatory elevation of glycogen levels following winter temperatures for this group, as suggested by Kleckner and Sidell (1985) in chain pickerel. The higher liver glycogen levels in May and July for the ABT group coincide with the compensatory growth noted in body mass and length for this group. The trend in Atlantic cod muscle glycogen is similar between the two groups, with levels in the CST group generally higher than that in the ABT group. The annual cycling of muscle glyco-

© 2005 NRC Canada

gen parallels levels of plasma glucose for the ABT group, with higher values in July and August and lower values in winter. The lowest value for muscle glycogen is in May, as reported by Mayerle and Butler (1971) in the American eel, just as ocean temperature begins to increase.

This long term study of Atlantic cod morphology and metabolism shows similar trends between the ABT and CST groups for most parameters studied, suggesting that photoperiod, which followed natural ambient light for each group, is the main factor controlling cod physiology, as suggested by Johnston et al. (2003) for Atlantic salmon. The temperature regime, per se, did not have a significant impact except to quantitatively change some of the parameters studied. The natural internal cycle of hormone and metabolite concentrations are maintained at least for the first 2 years of the Atlantic cod used in our experiment, regardless of the thermal conditions. Significant increases in tissue metabolites coincided with increases in body mass during the May to October period, implicating this as the period of most effective conversion of food to body mass when food is not limiting. Cod exposed to an ABT regime did demonstrate a compensatory growth period as water temperatures rose, as is consistent with depressed feeding at low temperatures. Although ABT cod demonstrated this added growth phase compared with the CST group, it was not enough to reach the mass or length of the CST group after 2 years. Thus, temperature appears to impact food utilization as food was provided ad libitum to each group in this experiment. Ambient photoperiod, therefore, is needed to obtain optimal growth and to maintain the physiological cycles needed to achieve this growth; repeating this experiment by manipulating photoperiod would be needed to further test this hypothesis. The patterns of tissue metabolites observed in this study could also be useful in defining the quantity and quality of feed used across the seasons in an aquaculture facility. Our results demonstrate that although there are quantitative differences in growth rates as a function of temperature, qualitative changes in most tissue metabolites of Atlantic cod follow seasonal changes contrary to photoperiod. Regardless of thermal history, and within the period and the parameters studied, constant temperature does not disturb normal seasonal cycles of the Atlantic cod. Our results also show that photoperiod is more important than food availability in controlling either metabolite storage or appetite (as we did not evaluate how much was eaten). Cod have a great capacity to acclimate to temperature changes, as only a few differences were observed between groups.

Acknowledgements

These studies were supported by funding from AquaNet, Network of Centres of Excellence, and the Natural Sciences and Engineering Research Council of Canada to Dr. J. Ballantyne, Dr. T.W. Moon, and Dr. W. Driedzic. We thank M. Lortie for assistance in metabolite analyses; V. French for lipid analyses; and T. MacCormick, J. Lewis, J. Treberg, and J. Bondy for assistance with tissue collection. Special appreciation is extended to Mr. D. Boyce and the staff of the Aquaculture Research and Development Facility, Ocean Sciences Centre for fish husbandry.

References

Bélanger, F., Blier, P.U., and Dutil, J.-D. 2002. Digestive capacity and compensatory growth in Atlantic cod (*Gadus morhua*). Fish Physiol. Biochem. **26**: 121–128.

Black, D., and Love, R.M. 1986. The sequential mobilization and restoration of energy reserves in tissues of Atlantic cod during starvation and refeeding. J. Comp. Physiol. B, **156**: 469–479.

Blier, P., and Guderley, H. 1988. Metabolic responses to cold acclimation in the swimming musculature of lake whitefish, *Coregonus clupeaformis*. J. Exp. Zool. **246**: 244–252.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua*). ICES J. Mar. Sci. **52**: 1–10.

Budge, S.M. 1999. Fatty acids biomarkers in cold water environment. Ph.D. thesis, Memorial University of Newfoundland, St John's, Newfoundland.

Copeman, L.A., Parrish, C.C., Harel, M., and Brown, J.A. 2002. Effects of docosahexaenoic, eicosapentaenoic, and arachidonic acids on the early growth, survival, lipid composition and pigmentation of yellowtail flounder (*Limanda ferruginea*): a live food enrichment experiment. Aquaculture, **210**: 285–304.

Dos Santos, J., Burkon, I.C., and Jobling, M. 1993. Patterns of growth and lipid deposition in cod (*Gadus morhua* L.) fed natural prey and fish based feeds. Aquaculture, **110**: 173–189.

Dutil, J.D., and Brander, K. 2003. Comparing productivity of North Atlantic cod (*Gadus morhua*) stocks and limits to growth production fish. Oceanography, **12**: 502–512

Folch, J., Lees, M., and Sloane Stanley, G.H. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. **226**: 497–509.

Foster, A.R., Houlihan, D.F., Hall, S.J., and Burren, L.J. 1992. The effects of temperature acclimatation on protein synthesis rates and nucleic acid content of juvenile cod (*Gadus morhua*) Can. J. Zool. **70**: 2095–2192.

Godo, O.R., and Haug, T. 1999. Growth rate and sexual maturity in cod (*Gadus morhua*) and Atlantic halibut (*Hippoglossus hippoglossus*). J. North Atl. Fish. Sci. **25**: 115–123.

Grant, S.M, Brown, J.A., and Boyce, D.L. 1998. Enlarged fatty livers of small juvenile cod: a comparison of laboratory-cultured and wild juveniles. J. Fish Biol. **52**: 1105–1114.

Guderley, H., and Gawlicka, A. 1992. Qualitative modification of muscle metabolic organization with thermal acclimation of rainbow trout, *Oncorhynchus mykiss*. Fish Physiol. Biochem. **10**: 123–132.

Guderley, H., Houle-Leroy, P., and Gagné, A. 2001. Thermal acclimation, growth, and burst swimming of threespine stickleback: enzymatic correlates and influence of photoperiod. Physiol. Biochem. Zool. **74**: 66–74.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A., and Andrews, J. 2004. Anlysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980–1999) using generalised additive models. Fish. Res. **70**: 17–25.

Henderson, R.J., and Tocher, D.R. 1987. The lipid composition and biochemistry of freshwater fish. Prog. Lipid Res. **26**: 281–347.

Hochachka, P.W., and Somero, G.N. 2002. Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press, Oxford, UK.

Jobling, M. 1988. A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. Aquaculture, **70**: 1–19.

Johnston, I.A., Manthri, S., Smart, A., Campbell, P., Nickell, D., and Alderson, R. 2003. Plasticity of muscle fiber number in sea-

© 2005 NRC Canada

water stages of Atlantic salmon in response to photoperiod manipulation. J. Exp. Biol. **206**: 3425–3435.

Kent, J., Koban, M., and Prosser, C.L. 1988. Cold-acclimation-induced protein hypertrophy in channel catfish and green sunfish. J. Comp. Physiol. B, **158**: 185–198.

Keppler, D., and Decker, K. 1974. Glycogen: determination with amyloglucosidase. *In* Methods of enzymatic analysis. Vol. 3. *Edited by* H.U. Bergmeyer. Verlag Chemie International, Deerfield Beach, Fla. pp. 1127–1131.

Kirsch, P.E., Iverson, S.J., and Bowen, W.D. 1998. Dietary effects on the fatty acid signature of whole Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **55**: 1378–1386.

Kleckner, N.W., and Sidell, B.D. 1985. Comparison of maximal activities of enzymes from tissues of thermally acclimated and naturally acclimatized chain pickerel (*Esox niger*). Physiol. Zool. **58**: 18–28.

Lambert, Y., and Dutil, J.-D. 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. Can. J. Fish. Aquat. Sci. **54**: 2388–2400.

Levesque, H.M., Bondy, J., Short, C., Ballantyne, J.S., Driedzic, W.R., and Moon, T.W. 2005. Effects of seasonal temperature and photoperiod on Atlantic cod (*Gadus morhua*). II. Enzymes of intermediary metabolism. Can. J. Fish. Aquat. Sci. **62**: 2864–2873.

Lilly, G.R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. ICES Mar. Sci. Symp. **193**: 133–146.

Martinez, M., Couture, P., and Guderley, H. 1999. Temporal changes in tissue metabolic capacities of wild Atlantic cod, *Gadus morhua* (L.), from Newfoundland. Fish Physiol. Biochem. **20**: 181–191.

Mayerle, J.A., and Butler, D.G. 1971. Effects of temperature and feeding on intermediary metabolism in North American eels (*Anguilla rostrata* LeSueur). Comp. Biochem. Physiol. A, **40**: 1087–1095.

McCormick, S.D., Moriyama, S., and Bjornsson, B.T. 2000. Low temperature limits photoperiod control of smolting in Atlantic salmon through endocrine mechanisms. Am. J. Physiol. Regul. Integr. Comp. Physiol. **278**: R1352–R1361.

Mishra, K., and Samantaray, K. 2004. Interacting effects of dietary lipid level and temperature on growth, body composition and fatty acid profile of rohu, *Labeo rohita* (Hamilton). Aquac. Nutr. **10**: 359–369.

Mommsen, T.P. 1998. Growth and metabolism. *In* The physiology of fishes. 2nd ed. *Edited by* D.H. Evans. CRC Press LLC, Boca Raton, Fla. pp. 65–97.

Morrison, W.R., and Smith, L.M. 1964. Preparation of fatty acid methyl esters and dimethylacetals from lipids with boron fluoride methanol. J. Lipid Res. **5**: 600–608.

Nanton, D.A., Lall, S.P., Ross, N.W., and McNiven, M.A. 2003. Effect of dietary lipid level on fatty acid β-oxidation and lipid composition in various tissues of haddock, *Melanogrammus aeglefinus* L. Comp. Biochem. Physiol. B, **135**: 95–108.

Parrish, C.C. 1987. Separation of aquatic lipid classes by chromarod thin-layer chromatography with measurement by Iatroscan flame ionization detection. Can. J. Fish. Aquat. Sci. **44**: 722–731.

Parrish, C.C. 1998. Determination of total lipid, lipid classes and fatty acids in aquatic samples. *In* Lipids in freshwater ecosystems. *Edited by* M.T. Arts and B.C. Wainman. Springer-Verlag, New York. pp. 4–12.

Pedersen, T., and Jobling, M. 1989. Growth rates of large sexually mature cod, *Gadus morhua*, in relation to condition and temperature during the annual cycle. Aquaculture, **81**: 161–168.

Pelletier, D., Guderley, H., and Dutil, J.-D. 1993. Effects of growth rate, temperature, season, and body size on glycolytic enzyme activity in the white muscle of Atlantic cod (*Gadus morhua*). J. Exp. Biol. **265**: 477–487.

Purchase, C.F., and Brown, J.A. 2001. Stock-specific changes in growth rates, food conversion efficiencies, and energy allocation in response to temperature change in juvenile Atlantic cod. J. Fish Biol. **58**: 36–52.

Seddon, W.L., and Prosser, C.L. 1997. Seasonal variations in the temperature acclimation response of the channel catfish, *Ictalurus punctatus*. Physiol. Zool. **70**: 33–44.

Shahidi, F., and Dunajski, E. 1994. Lipid fatty acids, growth and compositional characteristics of farmed cod (*Gadus morhua*). J. Food Lipids, **1**: 265–271.

Shcherbina, M.A., and Kazalauskene, O.P. 1971. Water temperature and digestibility of nutrient substances by carp. Hydrobiologia, **7**: 40–44.

Wendelaar Bonga, S.E. 1997. The stress response in fish. Physiol. Rev. **77**: 591–625.

© 2005 NRC Canada

Effects of seasonal temperature and photoperiod on Atlantic cod (*Gadus morhua*). II. Enzymes of intermediary metabolism

H.M. Levesque, J. Bondy, C. Short, J.S. Ballantyne, W.R. Driedzic, and T.W. Moon

Abstract: Atlantic cod (*Gadus morhua*) were held at either constant (~9 °C) or ambient ocean temperatures from December 2000 to June 2002 under natural photoperiod. The activities of gluconeogenic, glycolytic, lipid, and amino-acid-related enzymes were measured in liver and white muscle at eight time points over the experimental period. Principal component analysis reduced the 13 liver enzymes to two factors and the nine muscle enzymes to three factors. Factor scores were used to investigate the effects of season, temperature, and photoperiod on cod physiology. Liver factor I (FI) and muscle factor III (FIII) were significantly correlated with mass and length of the fish. Only liver FI was significantly correlated with tissue metabolites parameters. Significant differences between thermal groups were only observed for muscle FIII in June 2002. This study demonstrates that temperature is not a major factor determining the activity of the selected enzymes in ages-1+ to -3+ cod. Photoperiod and internal physiological cycles are more important in determining liver and muscle enzyme activities. Most liver enzymes measured are better indicators of fish growth than muscle enzyme, and liver protein is the parameter that best correlates with body mass, length, and liver mass.

Résumé : Des morues Atlantiques (*Gadus morhua*) ont été maintenues à une température constante (~9 °C) ou à la température océanique ambiante, de décembre 2000 jusqu'en juin 2002; les deux groupes ont été soumis à une même photopériode ambiante. Les activités des enzymes de la glyconéogenèse, de la glycolyse, du métabolisme des lipides et des protéines ont été mesurées dans le muscle blanc et le foie à huit reprises durant la période étudiée. Une analyse des composantes principales permis de réduire les 13 enzymes hépatiques à deux facteurs et les neuf enzymes musculaires à trois facteurs. Les positions de ces facteurs ont ensuite été utilisés pour rechercher les effets des saisons, des températures et de la photopériode sur métabolisme intermédiaire de la morue atlantique. Le facteur I (F1) du foie et le facteur III (F3) du muscle sont significativement corrélés à la masse et la longueur des poissons. F1 du foie est le seul facteur significativement corrélé aux métabolites tissulaires. Des différences significatives entre les groupes thermiques ont étés trouvées seulement chez F3 du muscle en juin 2002. Notre étude démontre que la température n'est pas un facteur déterminant majeur de l'activité des enzymes sélectionnées chez les morues âgées de +1 à +3 années. La photopériode et les cycles physiologiques internes sont plus importants pour déterminer l'activité enzymatique du foie et du muscle. La plupart des enzymes hépatiques mesurées sont de meilleurs indicateurs de la croissance des poissons que les enzymes musculaires. De plus, la quantité de protéines hépatiques est la variable le plus fortement corrélée à la masse et la longueur des poissons ainsi qu'à la masse du foie.

Introduction

Many environmental factors influence the activities of metabolic enzymes in animal tissues, including fish tissues. Primary among them are temperature, photoperiod, and food availability. Temperature is a known determinant of enzyme activities (Pelletier et al. 1993*a*) and also affects growth and developmental rates of teleosts (Ayala et al. 2001). Thermal acclimation leads many temperate zone species to adjust tissue metabolic capacity by enzyme changes (Jones and Sidell 1982; Guderley et al. 2001). Enzyme activities may also show seasonal variation (Martinez et al. 1999). Liver 3-hydroxyacyl coenzyme A dehydrogenase (HOAD) increased from July to September in the crucian carp (*Carassius carassius*), while lactate dehydrogenase (LDH) and cytochrome C oxidase (CCO; the enzyme catalyzing the last reaction in the electron transport chain) activities increased in July (Lind 1992). Muscle and liver metabolic organization

Received 1 September 2004. Accepted 27 May 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 15 November 2005.
J18294

H.M. Levesque[1] and T.W. Moon. Department of Biology, University of Ottawa, P.O. Box 450, Station A, Ottawa, ON K1N 6N5, Canada.
J. Bondy and J.S. Ballantyne. Department of Zoology, University of Guelph, Guelph, ON K1N 6N5, Canada.
C. Short and W.R. Driedzic. Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NL A1C 5S7, Canada.

[1]Corresponding author (e-mail: alevesqu@science.uottawa.ca).

 doi: 10.1139/F05-189 © 2005 NRC Canada

can also vary across seasons independently of temperature (Vezina and Guderley 1991), possibly reflecting an effect of reproductive activities, changing food availability, or photoperiod on enzyme activities. Guderley et al. (1996) showed that Atlantic cod (*Gadus morhua*) muscle LDH activities changed in response to feeding ration and to natural seasonal changes in food availability and environmental conditions. Glucose-6-phosphate dehydrogenase (G6PDH) also demonstrated laboratory acclimation in channel catfish (*Ictalurus punctatus*) liver (Kent et al. 1988).

Fish size or growth rate is also an important factor determining metabolic enzymes activities (Somero and Childress 1980; Martinez et al. 1999). Previous studies reported that muscle glycolytic and oxidative enzyme activities are correlated with fish body mass and length (Pelletier et al. 1993*a*, 1993*b*) and also vary along the length of the fish (Martinez et al. 2000). Atlantic cod intestinal CCO and citrate synthase (CS) activities also correlate with growth rate (Pelletier et al. 1994; Couture et al. 1998; Dutil et al. 1998). White muscle LDH, pyruvate kinase (PK), and CCO are positively correlated with growth in largemouth bass (*Micropterus salmoides*) and Atlantic cod (Goolish and Adelman 1987; Martinez et al. 1999, 2000). Aerobic and glycolytic capacities of muscle, liver, and intestine follow growth in mass of fish kept in the laboratory (Pelletier et al. 1995; Martinez et al. 1999). Enzyme activities also change during the life of an organism, and the expression of a positive allometric relationship of white muscle glycolytic enzymes are influenced by the physiological status of the fish and position along the length of the fish (Martinez et al. 1999, 2000).

The effects of seasonal temperature changes on Atlantic cod intermediary metabolism are poorly understood. The developing Atlantic cod aquaculture industry will require an understanding of this parameter to achieve success. Most previous studies looked at selected enzymes and correlated activities to changes in a limited number of environmental variables. Looking at selected enzymes may obscure changes in metabolic pathways. In an accompanying paper (Levesque et al. 2005), we demonstrated significant changes in a variety of body parameters and metabolites in Atlantic cod held at natural ocean temperatures and at a constant temperature (~9 °C) under natural photoperiod over an 18-month period. This study estimates activities of glycolytic, gluconeogenic, oxidative, electron transport chain, pentose phosphate pathway, and fatty acid enzymes in liver and white muscle and correlates these with the morphological and metabolic changes noted in this previous study. We predict that the observed changes in storage fuels and metabolites are correlated with enzyme activities associated with the pathways involved with these metabolites and the growth phases observed in the first paper. This experiment, when coupled with the companion paper (Levesque et al. 2005), represents a comprehensive analysis of growth and metabolic storage of Atlantic cod as a function of season and temperature variations.

Materials and methods

Experimental animals and procedure

Atlantic cod were held at the Ocean Sciences Centre (St. John's, Newfoundland and Labrador) aquaculture facilities under a natural photoperiod and were divided into two groups in late November. (See Levesque et al. (2005) for a detailed description of fish holding and husbandry.) One group was held under natural ocean water temperatures and the other group under a constant temperature (~9 °C), representing the lower end of the optimal growth temperature for Atlantic cod (Pelletier et al. 1993*a*). Ten cod from each group were sacrificed every 2–3 months by a blow to the head; total mass and length were determined; and samples of hypaxial white muscle (at the level of the dorsal fin) and liver were dissected and immediately frozen in liquid nitrogen and stored at –80 °C (see Levesque et al. (2005) for further details).

Enzyme activities

Enzyme activities were measured under saturating substrate conditions according to standard procedures (Moon and Mommsen 1987). Briefly, tissue pieces (0.1 g) were minced using a razor blade and homogenized (1:5 *w*/*v*) in a buffer containing 0.5 mol·L^{-1} glycerol, 20 mmol·L^{-1} Na_2HPO_4, 0.5 mmol·L^{-1} EDTA (ethylene diamine tetraacetic acid), 5 mmol·L^{-1} β-mercaptoethanol, 0.2% bovine serum albumin, and a cocktail of protease inhibitors (P-8340; Sigma Chemical Co., St. Louis, Missouri). Exceptions were made for CS, where the homogenizing buffer was 50 mmol·L^{-1} Tris–HCl (pH 7.4), and for HOAD, CCO, and carnitine palmitoyl transferase (CPT), where the homogenization buffer was 0.2% Triton X-100 in Tris–HCl buffer (pH 7.4). Homogenization was on ice by grinding the tissue in a 1.5 mL conical tube with a plastic pestle. The homogenate was centrifuged for 10 min at 4 °C and 10 000*g* (Micro Centaur, SANYO Scientific, Bensenville, Illinois); the resulting supernatant was used immediately for enzyme analysis. Reaction rates were assayed spectrophotometrically at 340 nm following the appearance or disappearance of NAD(P)H for all enzymes, except CS and CPT, which were monitored at 412 nm to detect the reduction of 5,5′-dithiobis(2-nitrobenzoic acid) (DTNB), and CCO, which was monitored at 550 nm following the reduction of oxidized cytochrome *c*. The extinction coefficients used for NAD(P)H, cytochrome *c*, and DTNB were 6.22, 19.1, and 13.61 mmol·L^{-1}·cm^{-1}, respectively. Enzyme activities were measured at room temperature (22 °C) using a plate reader (Spectra Max Plus 384; Molecular Devices, Sunnyvale, California) and SOFTmax pro software to calculate activities, except for the HOAD, CCO, and CPT, which were measured at 10 °C using a Cary/Varian 50 spectrophotometer (Varian Inc., Palo Alto, California). Substrate was added last to initiate the reaction; any activity in the absence of substrate was subtracted from total activity to give substrate-specific activities. Activities were corrected either for tissue weight or protein content using the bicinchoninic acid method (Sigma Chemical Co.).

All assays used 50 mmol·L^{-1} imidazole buffer (pH 7.8) with minor exceptions, and conditions were as follows: LDH (EC 1.1.1.27): NADH (0.15 m), pyruvate (5 mmol·L^{-1}); glutamate dehydrogenase (GDH; EC 1.4.1.3): α-ketoglutarate (0.875 mmol·L^{-1}), NADH (0.15 mmol·L^{-1}), ADP (1 mmol·L^{-1}), EDTA (0.1 mmol·L^{-1}), NH_4Cl (0.125 mmol·L^{-1}); malate dehydrogenase (MDH; EC 1.1.1.37): NADH (0.15 mmol·L^{-1}), oxaloacetate (0.5 mmol·L^{-1}); G6PDH (EC 1.1.1.49): $MgCl_2$ (10 mmol·L^{-1}), $NADP^+$ (0.5 mmol·L^{-1}), glucose 6-phosphate (1 mmol·L^{-1}); malic enzyme (ME; EC 1.1.1.40): $MgCl_2$ (10 mmol·L^{-1}), $NADP^+$ (0.5 mmol·L^{-1}), malate (1 mmol·L^{-1});

© 2005 NRC Canada

isocitrate dehydrogenase (IDH; EC 1.1.1.42): $MgCl_2$ (10 mmol·L^{-1}), $NADP^+$ (0.5 mmol·L^{-1}), isocitrate (2 mmol·L^{-1}); pyruvate kinase (PK; EC 2.7.1.40): KCl (25 mmol·L^{-1}), $MgCl_2$ (10 mmol·L^{-1}), NADH (0.15 mmol·L^{-1}), ADP (5 mmol·L^{-1}), phosphoenolpyruvate (PEP; 5 mmol·L^{-1}), excess PK-free LDH; phosphoenolpyruvate carboxykinase (PEPCK; EC 4.1.1.32): $MnCl_2$ (1.75 mmol·L^{-1}), 2-deoxyguanosine diphosphate (0.4 mmol·L^{-1}), $NaHCO_3$ (20 mmol·L^{-1}), PEP (5 mmol·L^{-1}), NADH (0.15 mmol·L^{-1}), excess MDH; aspartate aminotransferase (AST; EC 2.6.1.1): α-ketoglutarate (13 mmol·L^{-1}), aspartate (20 mmol·L^{-1}), NADH (0.15 mmol·L^{-1}), pyridoxal phosphate (2.5 mmol·L^{-1}), excess MDH; alanine aminotransferase (ALT; EC 2.6.1.2): α-ketoglutarate (13 mmol·L^{-1}), alanine (100 mmol·L^{-1}), NADH (0.15 mmol·L^{-1}), pyridoxal phosphate (2.5 mmol·L^{-1}), excess LDH; citrate synthase (CS; EC 4.1.3.7): Tris–HCl (50 mmol·L^{-1}, pH 8.0), DTNB (0.1 mmol·L^{-1}), acetyl-CoA (0.3 mmol·L^{-1}), oxalacetate (0.5 mmol·L^{-1}); 3-hydroxyacyl CoA dehydrogenase (HOAD; EC 1.1.1.35): acetoacetyl CoA (0.1 mmol·L^{-1}), NADH (0.1 mmol·L^{-1}); cytochrome *c* oxidase (CCO; EC 1.9.3.1): cytochrome *c* (sodium hydrosulfite-reduced) (50 μmol·L^{-1}); carnitine palmitoyl transferase (CPT; EC 2.3.1.21): DTNB (0.2 mmol·L^{-1}), palmitoyl CoA (0.1 mmol·L^{-1}), L-carnitine (0.5 mmol·L^{-1}).

Statistics

Statistical analyses were performed using SYSTAT (version 10, Systat Software Inc., Point Richmond, California) and SPLUS (version 8.0, Insightful Corporation, Seattle, Washington). Principal component analysis (PCA) was performed to reduce the number of variables (enzymes) by combining those that are correlated (i.e., express the same pattern of variations) (Jackson 2003). Liver and muscle enzyme PCA were followed by an oblimin rotation. Males and females were analyzed together except for gonad somatic index (GSI), as no gender differences were identified in the data set. One-way analyses of variance (ANOVA) were performed at each time point, and two separate one-way ANOVAs were performed on each treatment, on factors resulting from the PCA, and individual enzymes, with an adjusted critical value (α) of 0.00625, Bonferroni-corrected. When the one-way ANOVA showed significant effects, multiple mean comparisons were made using the Tukey–Kramer comparison. Simple correlations and multiple regressions were performed on enzyme factors and the morphological and metabolic parameters estimated in the previous paper (see Levesque et al. 2005); SYSTAT was used to assess their level of significance.

Results

PCA was performed as a means of grouping enzymes that showed the same pattern in the same tissue over the experimental period. However, this analysis is sensitive to factors that may vary over this period, particularly tissue mass and protein content. As noted in Levesque et al. (2005), liver mass, total protein, and hepatosomatic index (HSI) varied in a similar pattern, remaining low when cod growth rates were low but increasing and achieving a plateau as growth rates increased from August to October 2002. Muscle protein varied in a less predictable fashion. PCA was performed on enzyme activities expressed as either activity per milligram protein or per gram tissue mass or per whole organ (liver only). Depending upon the expression of activity, both the number of factors (enzyme groupings) and, in some cases, the specific enzymes represented by a particular factor changed. We decided to perform PCA on liver enzyme activities expressed as activity per whole liver (or activity per gram × total liver mass), as this estimates the total potential of the liver to catalyze a particular reaction. Muscle enzyme activities could not be reported in this manner, but are reported as activity per gram of muscle to reflect the potential of that enzyme in a unit of muscle mass.

Liver enzymes

Total liver enzyme activities are presented (Table 1). PCA reduced the 13 liver enzymes to two factors (Table 2), explaining approximately 85% of the variation of liver enzyme activities. All 13 liver enzymes contributed to each factor, but only enzymes that contributed more than 0.5 loading value to a particular factor were considered relevant to that factor. The closer the loading value to 1 (Table 2), the greater that enzyme contributes to that factor (Jackson 2003). Enzymes that contribute to the same factor are correlated. As noted in Table 2, CS, CCO, HOAD, and CPT all have loading values greater than 0.9 and are all grouped in factor I (FI); interestingly, these enzymes are exclusively found in the mitochondria. In addition, the amino-acid-related enzymes (ALT, AST, GDH), the gluconeogenic enzyme (PEPCK), the glycolytic enzyme (PK), and the NADPH-producing enzyme IDH contribute to FI more than to liver FII (Table 2). As these enzymes contribute the most to FI, this indicates that the activities of these enzymes followed the same trend and they are correlated. For each individual sample, PCA estimates a value for each factor that is a function of the contribution of all enzymes to that factor, which is then plotted as a function of sampling period. According to PCA, the more positive the factor is, the higher are the activities of the collective enzymes making up that factor (Jackson 2003). Enzymes contributing to FI had constant activities from December 2000 to August 2001, after which activities continuously increased until the final sampling point (June 2002). Liver FI enzymes were significantly different between sampling times ($P < 0.05$) but not between thermal groups (Fig. 1*a*). Liver CCO is included in FI and is presented as an example of the behaviour of each FI enzyme (Fig. 1*b*).

Liver FII is explained mainly by the dehydrogenases LDH and MDH and G6PDH, an NADPH-generating enzyme of the pentose–phosphate pathway. As with FI, FII enzyme activities were constant from December 2000 to August 2001, then generally increased from October to December 2001 and decreased to June 2002 (Fig. 2*a*). There were no activity differences between the ambient and constant temperature groups. Liver MDH is the enzyme most representative of FII enzymes and is presented here as a specific example of this factor (Fig. 2*b*).

Muscle enzymes

Total activities of nine muscle enzymes are presented (Table 3). Following PCA, activities of these nine enzymes

© 2005 NRC Canada

Table 1. Enzyme activities (mean ± standard error) in the liver of Atlantic cod (*Gadus morhua*) from December 2000 to February 2002.

		Dec. 2000		Feb. 2001		May 2001		July 2001	
		CST	ABT	CST	ABT	CST	ABT	CST	ABT
Gluconeogenic	PEPCK	15.44±4.86	15.92±4.85	11.37±4.85	10.59±5.11	8.91±4.85	2.35±4.85	16.66±5.12	8.93±5.12
Glycolytic	LDH*	1.47±0.85	1.07±0.85	0.88±0.85	0.62±0.89	1.77±0.85	0.68±0.85	1.36±0.95	1.03±0.89
	PK	100.95±28.98	98.73±28.98	75.49±28.98	72.69±30.55	71.40±28.98	35.67±28.98	84.39±30.55	58.76±28.98
Amino acid metabolism	ALT	171.05±53.55	177.82±53.55	77.43±56.45	91.56±53.55	53.82±53.55	24.77±53.55	154.7±56.45	75.12±53.55
	AST	123.64±29.22	152.66±29.22	83.08±29.22	67.87±30.80	49.78±29.22	11.65±29.22	108.55±30.80	67.24±29.22
Oxidative metabolism	CS	16.61±3.91	16.91±3.91	9.82±4.13	7.79±4.12	8.27±3.91	5.36±3.91	13.64±3.91	9.92±3.91
	GDH	84.38±24.74	98.04±24.74	59.37±24.74	48.19±26.07	81.25±24.74	36.66±24.74	96.21±26.07	58.04±24.73
	IDH	42.91±13.97	27.17±13.96	29.50±13.97	22.89±14.72	38.66±13.97	16±59±13.96	43.3±14.72	28.75±13.97
NADPH-producing	G6PDH	46.51±13.20	50.05±13.92	31.19±13.20	25.51±13.91	29.79±14.76	7.01±14.76	47.07±13.91	28.84±13.20
Lipid metabolism	CPT	5.59±7.79	8.50±7.79	11.96±8.33	10.41±7.79	17.64±7.79	2.88±7.79	34.58±8.33	26.30±7.79
	HOAD	6.70±5.99	5.99±5.99	15.63±5.99	14.64±5.99	22.63±6.40	5.22±6.40	34.17±6.92	22.73±6.40
		Aug. 2001		Oct. 2001		Feb. 2002		June 2002	
		CST	ABT	CST	ABT	CST	ABT	CST	ABT
Gluconeogenic	PEPCK	15.37±5.43	9.73±5.43	44.87±4.85	27.52±4.85	46.67±5.12	13.14±4.85	52.87±4.86	41.99±4.85
Glycolytic	LDH	0.87±0.95	0.48±0.95	8.51±0.85	4.16±0.85	8.89±0.85	8.66±0.85	7.74±0.85	7.09±0.85
	PK	101.81±32.40	54.39±32.40	197.61±28.98	132.63±28.98	287.03±28.98	219.65±28.98	347.36±28.98	383.99±28.99
Amino acid metabolism	ALT	129.21±69.13	71.57±59.87	324.48±53.55	226.28±53.55	618.81±53.5	336.14±53.55	729.81±53.55	488.39±53.55
	AST	109.68±32.67	60.04±32.67	235.07±29.22	169.72±29.22	407.25±29.22	288.85±29.22	353.22±29.22	306.98±29.22
Oxidative metabolism	CS	16.24±4.38	8.22±4.37	40.73±3.91	21.42±3.91	30.28±3.91	25.02±3.91	78.37±3.91	73.46±3.91
	GDH	116.42±27.65	47.11±27.66	187.20±24.74	132.86±24.74	240.52±24.74	149.05±24.74	244.07±24.74	169.26±24.74
	IDH	45.30±15.61	25.97±15.61	90.44±13.97	57.08±13.96	123.38±13.97	88.2±13.97	104.85±13.97	95.62±13.97
NADPH-producing	G6PDH	55.10±14.76	29.74±14.76	118.14±13.20	68.74±13.20	167.82±13.20	117.41±13.20	98.90±13.20	115.18±13.20
Lipid metabolism	CPT	7.79±7.79	10.71±7.79	24.61±8.33	9.15±8.33	45.82±7.79	45.17±7.79	82.02±7.79	54.89±7.79
	HOAD	5.99±5.99	12.02±5.99	40.19±5.99	23.61±5.99	50.26±5.99	68.81±5.99	77.09±5.99	68.80±5.99

Note: Liver cytochrome *c* oxidase (CCO) and liver malate dehydrogenase (MDH) activities are shown in Figs. 1 and 2, respectively, and are not presented here. Data are expressed as $\mu mol \cdot min^{-1} \cdot whole\ liver^{-1}$; an asterisk (*) indicates $mmol\ min^{-1} \cdot whole\ liver^{-1}$; $6 \geq n \geq 10$. Enzymes were assessed at 22 or 10 °C. CST, constant temperature (~9 °C); ABT, ambient temperature. Enzyme abbreviations are as follows: PEPCK, phosphoenolpyruvate carboxykinase; LDH, lactate dehydrogenase; PK, pyruvate kinase; ALT, alanine aminotransferase; AST, aspartate aminotransferase; CS, citrate synthase; GDH, glutamate dehydrogenase; IDH, isocitrate dehydrogenase; G6PDH, glucose-6-phosphate dehydrogenase; CPT, carnitine palmitoyl transferases; HOAD, 3-hydroxyacyl CoA dehydrogenase.

© 2005 NRC Canada

Table 2. Loading values (contribution) of liver enzymes for the two liver factors (principal components) and of muscle enzymes for the three muscle factors (principal components).

	Liver		Muscle		
Enzyme	Factor I	Factor II	Factor I	Factor II	Factor III
PEPCK	0.71618	0.31118	—	—	—
ALT	0.80225	0.25434	–0.484	0.753	–0.216
AST	0.68205	0.41512	0.345	0.708	–0.027
PK	0.85029	0.19487	0.923	0.061	0.008
LDH	0.48261	0.60778	0.868	0.049	–0.285
GDH	0.6665	0.38809	–0.020	0.079	0.778
MDH	–0.07480	0.92921	–0.126	–0.041	0.750
CS	0.93318	–0.07226	0.934	0.044	0.042
ME	—	—	0.120	0.710	0.168
IDH	0.62387	0.46031	0.332	0.604	0.330
G6PDH	0.47181	0.61771	—	—	—
CCO	0.96026	–0.05287	—	—	—
HOAD	0.98699	–0.17138	—	—	—
CPT	0.99019	–0.19484	—	—	—

Note: The closer the loading value is to 1, the higher the contribution of the enzyme to the factor. Abbreviations are as follows: PEPCK, phosphoenolpyruvate carboxykinase; ALT, alanine aminotransferase; AST, aspartate aminotransferase; PK, pyruvate kinase; LDH, lactate dehydrogenase; GDH, glutamate dehydrogenase; MDH, malate dehydrogenase; CS, citrate synthase; ME, malic enzyme; IDH, isocitrate dehydrogenase; G6PDH, glucose-6-phosphate dehydrogenase; CCO, cytochrome *c* oxidase; HOAD, 3-hydroxyacyl CoA dehydrogenase; CPT, carnitine palmitoyl transferases.

could be reduced to three factors accounting for approximately 80% of the variance in activities of these muscle enzymes. Muscle FI was explained by an oxidative metabolism enzyme (CS), an anaerobic metabolism enzyme (LDH), and a glycolytic enzyme (PK). Muscle FI activities remain constant from December 2000 to July 2001 and slowly increased to January 2002 and decreased to June 2002 (Fig. 3*a*). There were no differences between temperature treatments, and muscle FI was highly correlated to liver FII (Table 4). Muscle CS is included in muscle FI enzymes and is shown as an example of these FI enzymes (Fig. 3*b*).

Muscle FII includes two amino acid metabolism enzymes (ALT and AST) and two oxidative enzymes (IDH and ME). Muscle FII enzymes remained constant from December 2000 to July 2001, then increased until January 2002 and remained elevated through to June 2002 (Fig. 4*a*). Again there were no differences between temperature treatments. The activity of muscle ALT is included in muscle FII and is presented here as an example of FII enzymes (Fig. 4*b*).

Muscle FIII includes two oxidative enzymes (GDH and MDH). The activities of FIII enzymes remained stable from December 2000 to July 2001, then decreased and remained stable in the ambient temperature group, whereas they increased in January 2002 and decreased in June 2002 in the constant temperature group (Fig. 5*a*). A temperature effect is noted for muscle FIII enzymes at the January and June 2002 sampling points, with the constant temperature group showing significantly higher activities than the ambient group in January, a trend that was reversed in June 2002. MDH is included as an example of a muscle FIII enzyme (Fig. 5*b*).

Simple correlations and multiple regressions

We examined correlations among the factors (enzyme activity groupings) and the morphologic and metabolic parameters (see Levesque et al. 2005) obtained for individual cod at the different sampling times and temperature regimes (Table 4). Significant correlations were obtained among liver FI and muscle FIII and the morphological parameters estimated. Liver FI was also significantly correlated negatively with liver glycogen ($p < 0.01$) but positively with total liver protein ($p < 0.001$); muscle FI was significantly correlated with total liver glycogen ($p < 0.001$) (Table 4).

The most significant correlate of body mass and length was total liver protein (Table 5), which alone explained 60% and 57%, respectively, of the variability of body mass and length ($p < 0.001$). Liver FI and FII, condition factor, and HSI were also good indicators of cod body mass and (or) length, but their contribution was relatively small compared with liver protein (Table 5). The optimal multivariate model explained 86% of the variability in body mass and 77% of that in length. Adding more variables did not increase the coefficients of determination to a level that could justify their inclusion in the model. The optimal multivariate model for liver mass explained 92% of the variability in liver mass. Total liver protein was the most significant correlate of liver mass and alone explained 89% of the liver mass variation ($p < 0.001$). Total liver glycogen and liver FI and FII are also significant indicators of liver mass ($p < 0.001$; Table 5).

Discussion

Previous studies using Atlantic cod reported activities of numerous enzymes, and it is clear from these studies that activities vary depending on season, food availability, body mass, and physiological conditions. In fact, specific muscle enzymes were reported as useful indicators of growth in this species. These studies, however, examined enzymes at specific time points rather than using the same group of fish over an extended period of time. Our study sampled cod at eight time points across an 18-month period, beginning

© 2005 NRC Canada

Fig. 1. (*a*) General liver factor I pattern; (*b*) liver cytochrome *c* oxidase (CCO) (μmol·min^{-1}·whole liver^{-1}). Each point represents the mean ± standard error; $6 \geq n \geq 10$. ○, constant temperature cod (~9 °C); ●, ambient temperature cod; sampling dates are denoted by an arrowhead. Different letters indicate significant differences (Tukey–Kramer, $\alpha < 0.05$) within the constant temperature group (uppercase letters) and within the ambient temperature group (lowercase letters).

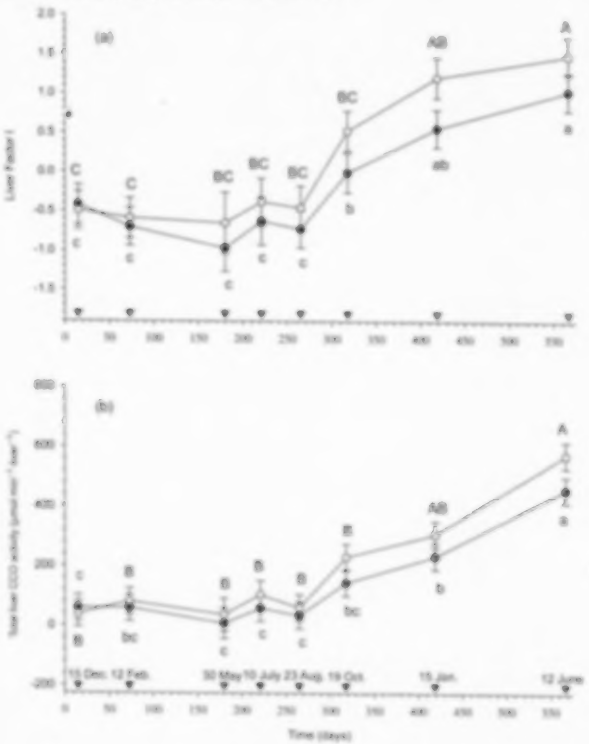
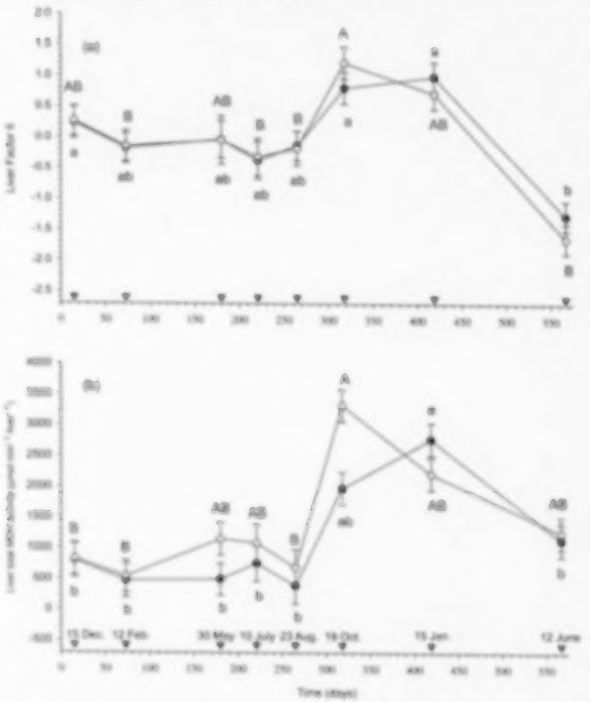


Fig. 2. (*a*) General liver factor II pattern; (*b*) liver malate dehydrogenase (MDH) activities (μmol·min^{-1}·whole liver^{-1}). Each point represents the mean ± standard error; $6 \geq n \geq 10$. ○, constant temperature cod (~9 °C); ●, ambient temperature cod; sampling dates are denoted by an arrowhead. Different letters indicate significant differences (Tukey–Kramer, $\alpha < 0.05$) within the constant temperature group (uppercase letters) and within the ambient temperature group (lowercase letters).



when the cod were age 1+ (20 months posthatch) and fed ad libitum. Growth and metabolite changes across this period better reflected changes in season–photoperiod than temperature, although cod held under a constant (~9 °C) versus a variable (ambient) thermal regime had higher growth. We predicted that these changes in growth and tissue metabolites reflect changes in tissue enzyme activities. Thirteen liver and nine muscle enzymes were analyzed, reflecting a variety of metabolic functions. PCA was used to reduce the number of variables (enzyme activities) and group together those enzymes that vary in a similar manner into the same factor. Liver factors defined from the PCA used in this study represented 85% of the variance in enzymes activities. However, depending on the expression of enzyme activity (i.e., units per milligram protein, per gram wet tissue weight, or per whole tissue), the number of factors defined by PCA deferred. This is based on the fact that liver mass, protein, and HSI, as well as muscle protein, vary across the sampling period (Levesque et al. 2005). The issue of how enzyme activities should be expressed in fish growth studies is discussed by Pelletier et al. (1995). Although correlations existed between enzyme activities and growth rate when expressed per gram wet muscle mass, the strongest correlation existed between growth and enzyme activity per microgram DNA. This study expressed liver enzyme activities per mass of liver to reflect the total potential activity of a particular enzyme in the liver. For white muscle, activities per gram of wet muscle mass were used, as Pelletier et al. (1995) did find a significant correlation between growth rate and this enzyme measure.

The 13 liver enzymes were reduced to two factors: FI and FII. Liver FI represented 10 of the 13 enzymes assayed, consisting of oxidative, glycolytic, and gluconeogenic enzymes. The pattern described for these enzymes reflected that noted for liver mass and total protein over the sampling period (see Levesque et al. 2005). Unfortunately, PCA did not group the enzymes into definable metabolic pathways that could assist in understanding activities of pathways responsible for the changes we noted in metabolite stores. This one liver factor (FI) was, however, significantly ($p < 0.01$) correlated with cod body mass and length, liver mass, and GSI, supporting a key role for the liver in the activities of muscle and gonad. Interestingly, there was a negative correlation with glycogen per gram liver. Liver glycogen content increases concurrently with the rise in cod growth rates, then declines even though liver mass remains high (see Levesque et al. 2005). Liver FI enzymes increased even though liver mass remained

© 2005 NRC Canada

Table 3. Enzyme activities (mean ± standard error) in the muscle of Atlantic cod (*Gadus morhua*) from December 2000 to February 2002.

		Dec. 2000		Feb. 2001		May 2001		July 2001	
		CST	ABT	CST	ABT	CST	ABT	CST	ABT
Glycolytic	PK	14.75±1.77	11.51±1.77	10.46±1.88	10.14±1.68	15.48±1.88	13.57±1.68	10.10±1.68	8.08±1.68
	LDH	209.1±18.9	192.5±18.9	99.2±20.0	88.7±17.9	142.7±17.9	136.0±17.9	137.4±17.9	103.04±17.9
Amino acid metabolism	AST	1.13±0.10	1.02±0.10	1.05±0.11	1.18±0.09	0.97±0.09	0.83±0.09	1.02±0.09	0.76±0.09
Oxidative metabolism	GDH	0.81±0.11	0.67±0.11	0.90±0.11	0.91±0.10	0.95±0.10	0.79±0.10	0.58±0.10	0.72±0.10
	IDH	4.61±0.31	4.21±0.31	3.09±0.33	3.48±0.29	3.08±0.29	2.99±0.29	2.99±0.29	2.97±0.29
	ME	0.46±0.03	0.39±0.04	0.39±0.04	0.40±0.03	0.46±0.03	0.46±0.03	0.35±0.03	0.34±0.03
		Aug. 2001		Oct. 2001		Feb. 2002		June 2002	
		CST	ABT	CST	ABT	CST	ABT	CST	ABT
Glycolytic	PK	13.95±1.88	13.61±1.88	22.75±1.68	14.16±1.68	23.11±1.68	23.41±1.68	4.73±1.68	4.46±1.68
	LDH	254.4±20.0	231.9±20.0	378.2±17.9	400.5±17.9	297.9±17.9	278.0±17.9	52.1±17.9	48.9±17.9
Amino acid metabolism	AST	1.02±0.11	0.91±0.11	0.95±0.09	0.93±0.09	0.85±0.09	0.75±0.09	1.87±0.09	1.25±0.09
Oxidative metabolism	GDH	0.43±0.11	0.59±0.12	0.21±0.10	0.45±0.10	1.08±0.10	0.68±0.10	0.39±0.10	0.67±0.10
	IDH	3.01±0.33	3.16±0.33	3.72±0.29	3.17±0.29	4.56±0.29	4.13±0.29	2.67±0.29	3.43±0.29
	ME	0.42±0.04	0.38±0.04	0.39±0.03	0.41±0.04	0.64±0.03	0.48±0.03	0.49±0.03	0.42±0.03

Note: Muscle citrate synthase (CS), alanine aminotransferase (ALT), and malate dehydrogenase (MDH) activities are shown in Figs. 3, 4, and 5, respectively, and are not presented here. Data are expressed as $\mu mol \cdot min^{-1} \cdot g^{-1}$ of tissue; $6 \geq n \geq 10$. Enzymes were assayed at 20 °C. CST, constant temperature (~9 °C); ABT, ambient temperature. Enzyme abbreviations are as follows: PK, pyruvate kinase; LDH, lactate dehydrogenase; AST, aspartate aminotransferase; GDH, glutamate dehydrogenase; IDH, isocitrate dehydrogenase; ME, malic enzyme.

Fig. 3. (*a*) General muscle factor I pattern; (*b*) muscle citrate synthase (CS) activities ($\mu mol \cdot min^{-1} \cdot g^{-1}$ tissue). Each point represents the mean ± standard error; $6 \geq n \geq 10$. ○, constant temperature cod (~9 °C); ●, ambient temperature cod; sampling dates are denoted by an arrowhead. Different letters indicate significant differences (Tukey–Kramer, $\alpha < 0.05$) within the constant temperature group (uppercase letters) and within the ambient temperature group (lowercase letters).

stable, providing further evidence that the liver serves as a tissue fuel source for the rest of the fish body. The oxidative enzymes (CS, HOAD, CPT, and CCO) were included in liver FI, and their loading values were high relative to the other enzymes found in this factor. The high loading values for these particular enzymes implicated the role of lipid oxidation in providing energy for growth in the cod. The fact that liver FI is correlated with liver total protein and liver mass indicated a strong effect of photoperiod, as liver mass and liver total protein are inversely following photoperiod variations (see Levesque et al. 2005).

Liver FII is represented by three dehydrogenases (G6PDH, LDH, and MDH), whose activities are generally high throughout the sampling period, increase concomitantly with the rapid rise in growth rate, and then fall as growth rates decline. This pattern is not correlated with any body parameter or tissue metabolite measured. One of these enzymes (LDH) has previously been shown in muscle to be the strongest correlate of growth rates in cod (Pelletier et al. 1995; Martinez et al. 1999), probably based on the well-established relationship between size and metabolic capacities (Somero and Childress 1980; Sullivan and Somero 1983). Our study suggests that enzymes other than muscle LDH might also be good indicators of growth rates.

The muscle enzymes expressed as units per gram white muscle could be reduced to three factors representing 80%

© 2005 NRC Canada

Table 4. Correlations between liver and muscle enzyme factors and morphometric parameters and tissue metabolites in Atlantic cod (*Gadus morhua*).

Variable	LFI	LFII	MFI	MFII	MFIII
Mass (g)	0.70414**	–0.03194	0.02118	0.22721	–0.42894*
Length (cm)	0.68407**	–0.03575	0.08846	0.22859	–0.43218*
Liver mass (g)	0.64573**	0.13333	0.2416	0.30186	–0.28833
HSI	0.20542	0.33096	0.35624**	0.11631	0.07378
GSI	0.43315*	–0.25661	–0.30738	–0.00751	–0.28085
CF	0.46837**	0.13158	0.08803	0.1563	–0.30919
Muscle protein ($mg \cdot g^{-1}$)	–0.31382	–0.05371	0.01867	–0.05547	0.25129
Liver protein ($mg \cdot g^{-1}$)	–0.36568	0.01281	0.03988	–0.10824	–0.04985
Total liver protein ($mg \cdot g^{-1}$)	0.58587**	0.18995	0.34454	0.27977	–0.41081
Muscle glycogen ($mg \cdot g^{-1}$)	–0.05854	0.00246	0.12935	0.03793	–0.16342
Liver glycogen ($mg \cdot g^{-1}$)	–0.40436*	0.12668	0.22877	–0.15916	–0.09645
Total liver glycogen	0.14223	0.37325	0.53031**	0.23143	–0.28020
Glucose ($mmol \cdot L^{-1}$)	–0.25548	0.16984	0.15556	–0.00695	–0.05169
Lactate ($mmol \cdot L^{-1}$)	–0.30874	0.12293	0.05191	–0.09020	0.23418
Tiglycerid	0.11784	0.29715	0.42638	0.22422	–0.21371
Total lipids	0.09412	0.32062	0.42578	0.16194	–0.18416
LFI	—	—	–0.07630	0.26292	–0.34535
LFII	—	—	0.49780**	0.01834	0.01543

Note: Bonferroni probabilities are as follows: *, $p < 0.05$; **, $p < 0.001$. LF, liver factor; MF, muscle factor; HSI, hepatosomatic index; GSI, gonad somatic index; CF, condition factor.

Fig. 4. (*a*) General muscle factor II pattern; (*b*) muscle alanine aminotransferase (ALT) activities ($\mu mol \cdot min^{-1} \cdot g^{-1}$ tissue). Each point represents the mean ± standard error; $6 \geq n \geq 10$. ○, constant temperature cod (~9 °C); ●, ambient temperature cod; sampling dates are denoted by an arrowhead. Different letters indicate significant differences (Tukey–Kramer, $\alpha < 0.05$) within the constant temperature group (uppercase letters) and within the ambient temperature group (lowercase letters).

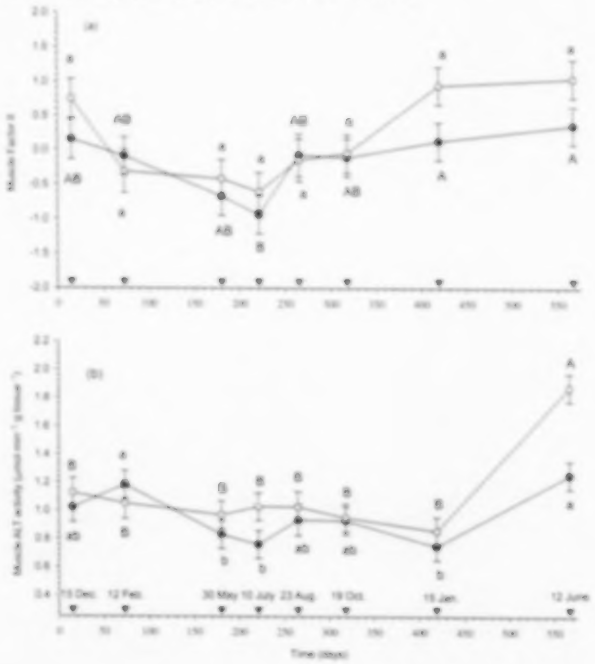
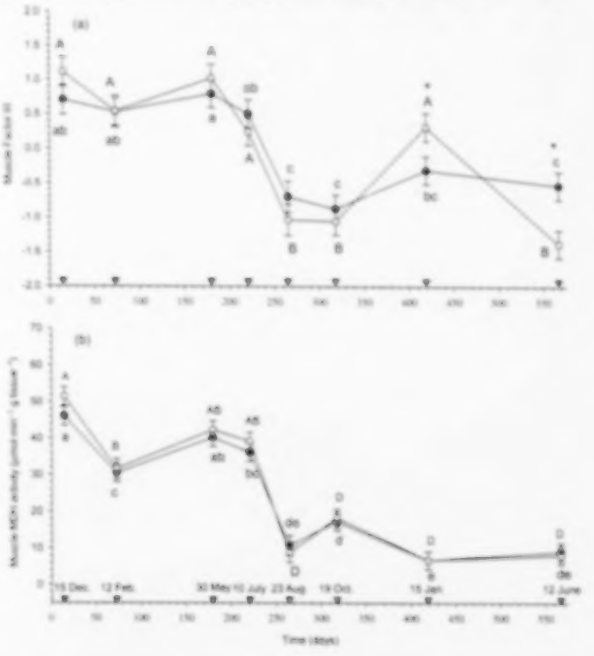


Fig. 5. (*a*) General muscle factor III pattern; (*b*) muscle malate dehydrogenase (MDH) activities ($\mu mol \cdot min^{-1} \cdot g^{-1}$ tissue). Each point represents the mean ± standard error $6 \geq n \geq 10$. ○, constant temperature cod (~9 °C); ●, ambient temperature cod; sampling dates are denoted by an arrowhead. Different letters indicate significant differences (Tukey–Kramer, $\alpha < 0.05$) within the constant temperature group (uppercase letters) and within the ambient temperature group (lowercase letters). An asterisk (*) indicates differences between ambient and constant temperature groups at a particular sampling time (Tukey–Kramer, $\alpha < 0.05$).



© 2005 NRC Canada

Table 5. Multiple regression models utilizing the variables that best explain the variability of mass, length, and liver mass in Atlantic cod (*Gadus morhua*).

	Variable								
	N	R^2	Intercept	LFI	LFII	CF	HSI	Total liver glycogen	Total liver protein
Mass	105	0.866	71.90	106.67	−56.18	37968.78	−5413.31	—	247.38
Contribution (%)	—	—	—	11.7	3.0	4.0	7.0	—	60.7
p	—	—	<0.001	<0.001	<0.001	<0.001	<0.001	—	<0.001
Length	105	0.77	31.54	2.56	−1.12	—	−86.93	—	6.68
Contribution (%)	—	—	—	11.2	2.6	—	6.5	—	57.2
p	—	—	<0.001	<0.001	<0.001	—	<0.001	—	<0.001
Liver mass	105	0.927	−12.22	4.09	−2.06	—	—	9.74	18.11
Contribution (%)	—	—	—	1.5	1.2	—	—	1.0	89.0
p	—	—	<0.001	<0.001	<0.001	<0.001	—	<0.001	<0.001

Note: *N*, number in sample; R^2, correlation factor; LF, liver factor; CF, condition factor; HSI, hepatosomatic index.

of the variance in activities. Again, as with the liver factors, the enzymes did not group into clearly definable metabolic pathways. Muscle FI and FII enzymes remain relatively constant throughout the 18-month sampling period with two exceptions: (*i*) muscle FI increases dramatically just before the peak growth period and then quickly decreases, and (*ii*) FII enzymes also rise before the peak growth period but remain constant as FI enzymes fall. The increase in FI enzymes, including LDH, supports previous work that demonstrated a strong correlation between LDH activities and growth rates in cod (Martinez et al. 1999). The period January to June 2002 represents a slow growth period for cod (see Levesque et al. 2005) and a period when the GSI is significantly ($p < 0.01$) increasing. A decrease in muscle FI enzymes (PK, LDH, CS) would reduce oxidation of carbon, while high activities of some FII enzymes (in particular ALT, AST) would enhance muscle protein breakdown, ultimately providing additional synthetic carbon for gonadal anabolism. Certainly, muscle FI is also correlated with both HSI and total liver glycogen, which may also be important for increases in GSI. Muscle FIII enzymes (GDH, MDH) are negatively correlated with body mass and length, as would be expected by the sharp decline in activities at a time when cod are actively growing. The precise reason for this pattern is still under investigation.

A major conclusion from this study is that temperature has little impact on the activities of the assayed enzymes. With one exception (muscle FIII, last two sampling points), there were no activity differences between holding the cod at a constant (~9 °C) versus a variable (ambient) temperature regime. Although temperature has a direct impact on enzyme activities (Hazel and Prosser 1974), it is clear from this study that such activities when measured at the same temperature are unaffected by water temperature, suggesting that the activities measured here are thermally compensated (Seddon and Prosser 1997) to facilitate optimal performance at all temperatures (Guderley et al. 2001). This appears true of both mitochondrial and cytosolic enzymes. This implies that the pattern of enzyme activities shown here is responding to other conditions that are changing over the sample period.

Growth in length necessarily involves the synthesis of structural molecules, whereas growth in mass can include restoration and accumulation of energy reserves (Couture et al. 1998). Growth in length appears to dominate in young fish, whereas growth in mass becomes relatively important as fish reach adulthood (Ricker 1979). Growth in length is also more permanent than growth in mass, as food deprivation leads to loss of body mass (Couture et al. 1998). In our study, the regression found for body mass and length is very similar. Both liver FI and FII, HSI, and total liver protein explain the most mass and length variation in the cod studied. Allometries of white muscle glycolytic enzymes are not always found, depending on size, reproductive state, and season of sampling (Martinez et al. 1999), and allometry of enzyme activities changes during an organism's life. For example, Martinez et al. (1999) reported a higher allometric relationship in Newfoundland cod in fall and early winter. Our data indicate that lipid catabolism is enhanced during the period of enhanced growth that occurred from August 2001 to October 2001 (see Levesque et al. 2005) and when photoperiod is increasing, as previously reported by Jones and Sidell (1982). None of the muscle factors is included in mass and length multiple regression, but MF3 is significantly ($p < 0.05$) correlated with fish mass and length. This finding is contrary to previous research, which reported a positive correlation between the activity of muscle CS (Mathers et al. 1992; Pelletier et al. 1993*a*) and glycolytic enzymes (Sullivan and Somero 1983; Pelletier et al. 1994; Dutil et al. 1998) with growth rate. In our study, growth in mass and length were mainly explained by total liver protein content. HSI plays an important role in fish mass regression, but this may be an artifact, as organ mass and fish mass are always highly correlated (Pelletier et al. 1994). Unfortunately, it was not possible to include liver lipids into the regression because of the low data number (only five per group).

In conclusion, the pattern of enzyme activities studied here generally reflects changes in organ mass and growth rates or the physiological changes occurring within the cod over the sampling period. There are few direct affects of the thermal regime at which the cod were held. As we previously noted (Levesque et al. 2005), photoperiod is a prime driver of cod physiology, with the temperature regime having a limited quantitative impact on the outcome. Examining enzymes does not assist our understanding of the differences

© 2005 NRC Canada

noted in growth rates between the constant and variable temperature groups. The PCA technique is effective in studies of this kind containing multiple variables that may affect distinct processes Unfortunately, this technique did not provide additional information correlating enzyme activities to changes in specific metabolites. What it does suggest, however, is that a limited number of patterns of enzyme variation exist and that some factor(s) may generate these patterns. This study and the companion paper (Levesque et al. 2005) integrate the changes in morphometry, metabolites, and enzyme activities in young cod throughout the year. This is the first time that so many physiological and morphological factors are studied in cod for 18 months and are integrated together. Given the low temperature encountered during the winter in Atlantic Canadian waters, it is important to understand the interactions among temperature, growth, and intermediary metabolism if growth is to be optimized in cultivated Atlantic cod.

Acknowledgments

These studies were supported by funding from AquaNet, Network of Centres of Excellence, and the Natural Sciences and Engineering Research Council of Canada to Dr. J. Ballantyne, Dr. T.W. Moon, and Dr. W. Driedzic. We thank M. Lortie for assistance in enzyme mesurements and T. MacCormick, J. Lewis, and J. Treberg for assistance with tissue collection.

References

Ayala, M.D., López-Albors, O., Gil, F., García-Alcazar, A., Abellán, E., Alarcón, J.A., Álvarez, M.C., Ramírez-Zarzosa, G., and Moreno, F. 2001. Temperature effects on muscle growth in two populations (Atlantic and Mediterranean) of sea bass, *Dicentrarchus labrax* L. Aquaculture, **202**: 359–370.

Couture, P., Dutil, J.-D., and Guderley, H. 1998. Biochemical correlates of growth and condition in juvenile Atlantic cod (*Gadus morhua*) from Newfoundland. Can. J. Fish. Aquat. Sci. **55**: 1591–1599.

Dutil, J.D., Lambert, Y., Guderley, H., Blier, P.U., Pelletier, D., and Desroches, M. 1998. Nucleic acids and enzymes in Atlantic cod (*Gadus morhua*) differing in condition and growth rate trajectories. Can. J. Fish. Aquat. Sci. **55**: 788–795.

Goolish, E.M., and Adelman, I.R. 1987. Tissue-specific cytochrome oxidase activity in largemouth bass: the metabolic costs of feeding and growth. Physiol. Zool. **60**: 454–464.

Guderley, H., Dutil, J.-D., and Pelletier, D. 1996. The physiological status of Atlantic cod, *Gadus morhua*, in the wild and the laboratory: estimates of growth rates under field conditions. Can. J. Fish. Aquat. Sci. **53**: 550–557.

Guderley H., Leroy, P.H., and Gagné, A. 2001. Thermal acclimation, growth, and burst swimming of threespine stickleback: enzymatic correlates and influence of photoperiod. Physiol. Biochem. Zool. **74**: 66–74.

Hazel, J.R., and Prosser, C.L. 1974. Molecular mechanisms of temperature compensation in poikilotherms. Physiol. Rev. **54**: 620–677.

Jackson, J.E. 2003. A user's guide to principal components. John Wiley & Sons, Inc., Hoboken, N.J.

Jones, P.L., and Sidell, B.D. 1982. Metabolic responses of striped bass (*Morone saxatilis*) to temperature acclimation. II. Alterations in metabolic carbon source and distributions of fiber types in locomotory muscle. J. Exp. Zool. **219**: 163–171.

Kent, J., Koban, M., and Prosser, C.L. 1988. Cold-acclimation-induced protein hypertrophy in channel catfish and green sunfish. J. Comp. Physiol. B, **158**: 185–198.

Levesque, H.M., Short, C., Moon, T.W., Ballantyne, J.S., and Driedzic, W.R. 2005. Effects of seasonal temperature and photoperiod on Atlantic cod (*Gadus morhua*). I. Morphometric parameters and metabolites. Can. J. Fish. Aquat. Sci. **62**: 2854–2863.

Lind, Y. 1992. Summertime and early autumn activity of some enzymes in the carbohydrate and fatty acid metabolism of the crucian carp. Fish Physiol. Biochem. **9**: 409–415.

Martinez, M., Couture, P., and Guderley, H. 1999. Temporal changes in tissue metabolic capacities of wild Atlantic cod, *Gadus morhua* (L.), from Newfoundland. Fish Physiol. Biochem. **20**: 181–191.

Martinez, M., Dutil, J.-D., and Guderley, H. 2000. Longitudinal and allometric variation in indicators of muscle metabolic capacities in Atlantic cod (*Gadus morrhua*). J. Exp. Zool. **287**: 38–45.

Mathers, E.M., Houlihan, D.F., and Cunningham, M.J. 1992. Nucleic acid concentrations and enzyme activities as correlates of growth rate of the saithe *Pollachius virens*: growth-rate estimates of open-sea fish. Mar. Biol. **112**: 363–369.

Moon, T.W., and Mommsen, T.P. 1987. Enzymes of intermediary metabolism in tissues of little skate, *Raja erinacea*. J. Exp. Zool. **58**: 9–15.

Pelletier, D., Guderley, H., and Dutil, J.-D. 1993*a*. Effects of growth rate, temperature, season and body size on glycolytic enzyme activities in the white muscle of Atlantic cod (*Gadus morhua*). J. Exp. Zool. **265**: 477–487.

Pelletier, D., Guderley, H., and Dutil, J.-D. 1993*b*. Does the aerobic capacity of fish muscle change with growth rates? Fish Physiol. Biochem. **12**: 83–93.

Pelletier, D., Dutil, J.-D., and Guderley, H. 1994. Relation between growth rate and metabolic organization of white muscle, liver and digestive tract in cod, *Gadus morhua*. J. Comp. Physiol. B, **164**: 179–190.

Pelletier, D., Blier, P.U., Dutil, J.-D., and Guderley, H. 1995. How should enzyme activities be used in fish growth studies? J. Exp. Biol. **198**: 1493–1497.

Ricker, W.E. 1979. Growth rates and models. *In* Fish physiology. Chapter 8. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York. pp. 677–743.

Seddon, W.L., and Prosser, C.L. 1997. Seasonal variations n the temperature acclimation response of the channel catfish, *Ictalurus punctatus*. Physiol. Zool. **70**: 33–44.

Somero, G.N., and Childress, J.J. 1980. A violation of the metabolism-size scaling paradigm: activities of glycolytic enzymes increase in larger-size fish. Physiol. Zool. **53**: 322–327.

Sullivan, K.M.,and Somero, G.N. 1983. Size- and diet-related variations in enzymatic activity and tissue composition in the sablefish, *Anoplopoma fimbria*. Biol. Bull. (Woods Hole), **164**: 135–326.

Vezina, D., and Guderley, H. 1991. Anatomic and enzymatic responses of the 3-spined stickleback, *Gasterosteus aculeatus*, to thermal acclimation and acclimatization. J. Exp. Biol. **258**: 277–282.

© 2005 NRC Canada

The importance of Colorado River flow to nursery habitats of the Gulf corvina (*Cynoscion othonopterus*)

Kirsten Rowell, Karl W. Flessa, David L. Dettman, and Martha Román

Abstract: We test the hypothesis that Colorado River flow is important in providing nursery habitat for the Gulf corvina (*Cynoscion othonopterus*), a commercially valuable and endemic fish in the upper Gulf of California. We use oxygen isotopes in otoliths to determine when these fish inhabit isotopically different bodies of water (Gulf of California versus the Colorado Estuary). The $\delta^{18}O$ values in the natal otoliths of *C. othonopterus*, significantly more negative than can be predicted by temperature alone, provide evidence that this species uses the brackish habitats created by flow of the Colorado River. A significant log-linear relationship between the natal $\delta^{18}O$ values and the cumulative flow of the Colorado River during natal development confirms use of brackish habitat in years that the Colorado River water reached the Gulf. Natal $\delta^{18}O$ values indicate that *C. othonopterus* seek out estuarine habitats with salinities between 26‰ and 38‰. Reduction in Colorado River flow since the construction of upstream dams has reduced the size of nursery habitat for *C. othonopterus*. Our results support the hypothesis that declines in commercial landings can be at least partially attributed to reduced river flow. Increased flow would increase nursery habitat and likely benefit recruitment.

Résumé : Nous évaluons l'hypothèse selon laquelle le débit du Colorado joue un rôle important dans l'établissement de l'habitat de nursery pour l'acoupa du golfe (*Cynoscion othonopterus*), un poisson endémique d'importance commerciale dans la partie supérieure du golfe de Californie. L'analyse des isotopes d'oxygène dans les otolithes nous permet de déterminer si ces poissons habitent le golfe de Californie ou l'estuaire du Colorado, des eaux distinctes par leurs isotopes. Les valeurs significativement plus négatives de $\delta^{18}O$ des otolithes de naissance de *C. othonopterus* qu'on ne peut expliquer par la seule température sont des preuves que cette espèce utilise les eaux saumâtres crées par le débit du Colorado. Il existe une relation logarithmique linéaire entre les valeurs natales de $\delta^{18}O$ et le débit cumulé du Colorado durant le développement natal, ce qui confirme l'utilisation des eaux saumâtres les années où l'eau du Colorado atteint le golfe. Les valeurs natales de $\delta^{18}O$ indiquent que *C. othonopterus* recherche les habitats estuariens à salinité comprise entre 26 ‰ et 38 ‰. La réduction du débit du Colorado depuis la construction de barrages en amont a rétréci la taille de l'habitat de nursery de *C. othonopterus*. Nos résultats appuient l'hypothèse qui veut que les diminutions des débarquements commerciaux soient en partie attribuables au débit réduit du fleuve. Une augmentation du débit accroîtrait l'habitat de nursery et améliorait vraisemblablement le recrutement.

[Traduit par la Rédaction]

Introduction

Many of the world's rivers, including the Nile, Yellow, Indus, Amu, Syr, and Colorado, no longer reach the ocean in most years, compromising key habitats that sustain bird populations, fisheries, and coastal fishing communities (Drinkwater and Frank 1994; Gleick 2003). The elimination of important spawning and nursery estuarine habitat as a result of reduced river flows has been documented as one of the major causes of the crashes of several fisheries (sardine, shrimp, and several species of sciaenids) (see references in Drinkwater and Frank (1994) and Grimes and Kingsford (1996)). As humans continue to alter natural river flows to the ocean, we are beginning to recognize the profound importance of naturally flowing rivers to estuaries and healthy marine systems (Fransz 1986; Drinkwater and Frank 1994; Grimes and Kingsford 1996). In this paper, we use oxygen isotopes in otoliths to investigate how the reduction of Colorado River flows may have contributed to the commercial extinction of the economically important Gulf corvina

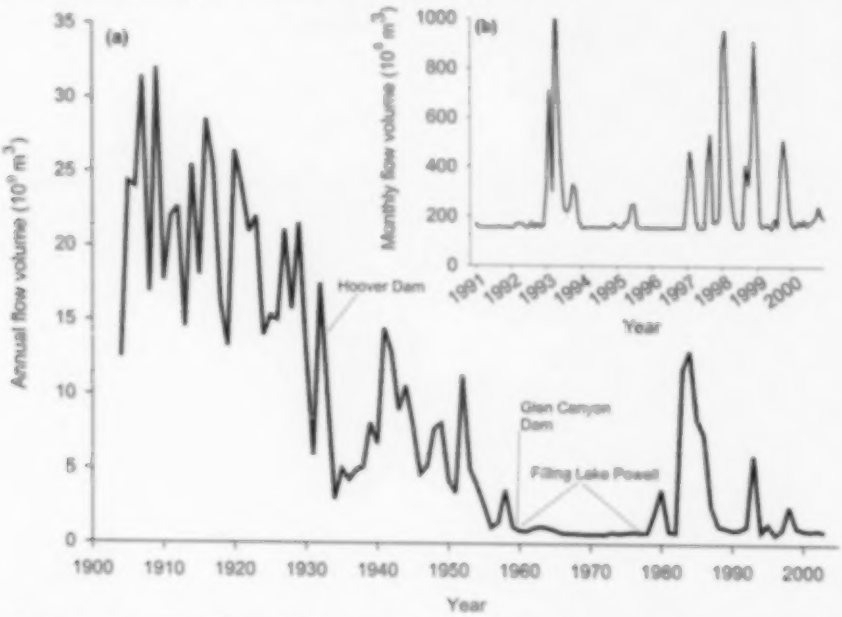
Received 12 January 2005. Accepted 7 September 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 10 November 2005.
J18500

K. Rowell,[1,2] K.W. Flessa, and D.L. Dettman. Department of Geosciences, University of Arizona, Tucson, AZ 85721, USA.
M. Román. Comision de Ecologia y Desarrollo Sustentable del Estado de Sonora, P.O. Box 12228, San Luis, AZ 85349, USA.

[1]Corresponding author (e-mail: krowell@geo.arizona.edu).
[2]Present address: Department of Biology, University of Washington, Seattle, WA 98195-1800, USA.

 doi: 10.1139/F05-193 © 2005 NRC Canada

Fig. 1. (*a*) Colorado River annual flow volume (10^9 m^3) below Yuma Main Canal Wasteway at Yuma, Arizona, USA (station 09521100), for years 1904–2003; (*b*) Colorado River monthly flow volume (10^6 m^3) for years 1991–2002. Years where the hydrograph is flat depict the annual flow of 1.8×10^9 m^3 required by the 1944 Mexican Water Treaty.



(*Cynoscion othonopterus* Jordan and Gilbert 1882) in the upper Gulf of California. We hypothesize that the Colorado River flow is instrumental in providing spawning and nursery habitat to Gulf corvina.

Before the construction of upstream dams and water diversions in the 1930s, the Colorado River was a major influence on the upper Gulf of California, creating extensive wetlands and a large estuary (Lavín and Sánchez 1999; Glenn et al. 2001). Today, the Colorado River rarely flows into the Gulf of California (Fig. 1). The lack of historic baseline biotic and abiotic information has made it difficult to quantify the effects of the dramatic reduction in flow on the estuarine ecosystems; however, upstream alterations of Colorado River flow are commonly cited as a significant threat to biodiversity in the upper Gulf of California (Musick et al. 2000; Glenn et al. 2001; Brusca et al. 2005). In addition, several endemic species in the upper Gulf and Colorado River Delta are endangered, including the large sciaenid *Totoaba macdonaldi*, the Gulf of California harbor porpoise (*Phocoena sinus*), and the Yuma clapper rail (*Rallus longirostris yumanensis*) (Cisneros-Mata et al. 1995; Gallo-Reynoso 1998; D'Agrosa et al. 2000). Other species may have also been adversely affected by reduced river flow. For example, the population and distribution of the endemic bivalve mollusc *Mulinia coloradoensis*, which is restricted to the area influenced by the river's freshwater plume, has shrunk significantly (Rodriguez et al. 2001*a*, 2001*b*; Kowalewski et al. 2000).

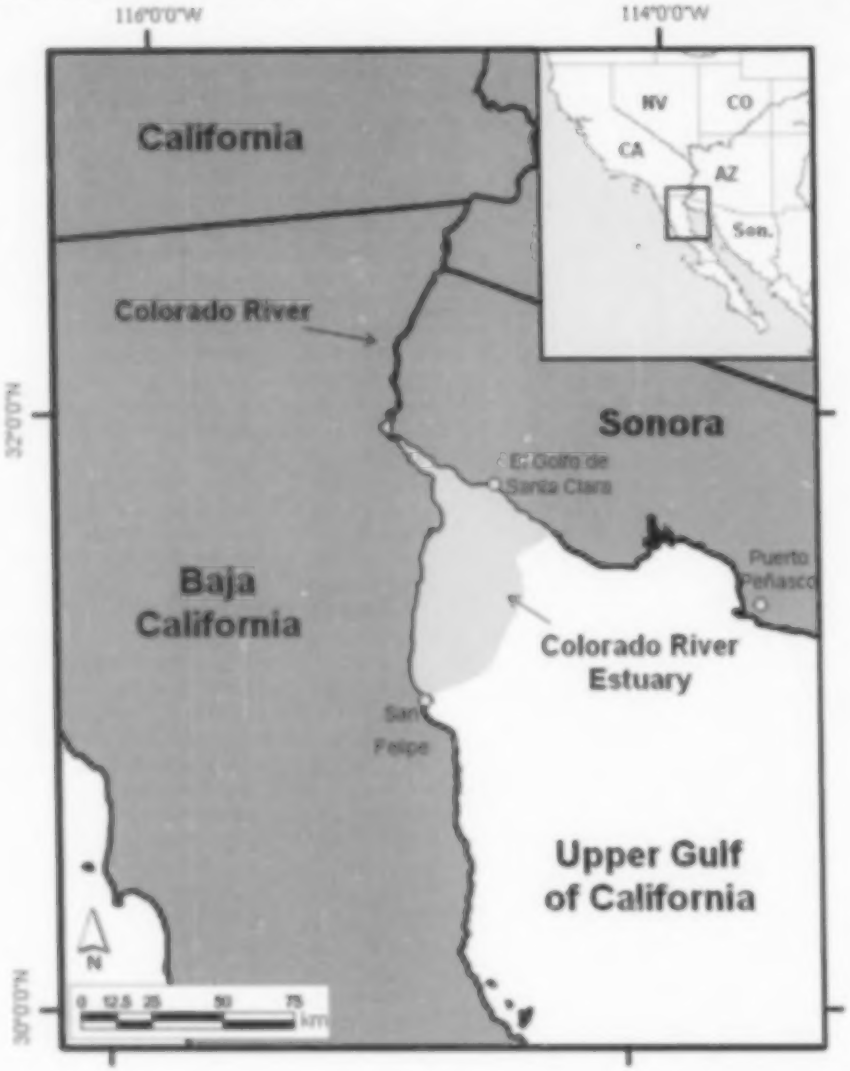
The Gulf corvina became commercially extinct in the early 1960s (Román 1998; Román et al. 1998), when river flow to the Gulf effectively ceased (Fig. 1). In 1993, a controlled release of Colorado River water dramatically increased flows to the Gulf of California (Fig. 1), and in the three years after the release, *C. othonopterus* catches increased from 32 to 1278 metric tons (t) in the fishing village of El Golfo de Santa Clara, Sonora, Mexico (M. Román, unpublished data). This substantial rebound in the Gulf corvina catch suggests that Colorado River flow is important to the reproductive success of the fish. Large pulses of Colorado River water that reached the Gulf of California also occurred in 1983–1986 (Fig. 1); however, catch data for that period do not exist. Although overfishing may have been a major cause of the Gulf corvina's previous commercial extinction, reduction in Colorado River flow may have also contributed to its decline by reducing the size of its nursery habitat. The American Fisheries Society lists *C. othonopterus* as a vulnerable species because of overfishing and changes to its estuarine spawning grounds caused by upstream diversions of Colorado River water (Musick et al. 2000).

Gulf corvina is endemic to the upper Gulf of California. Other species of the family Sciaenidae are known to use estuaries for spawning and nursery sites (Chao 1978; Blaber 1997; Fennessy 2000). Much of what is known about *C. othonopterus* is from traditional knowledge of fishermen. *Cynoscion othonopterus* live between 7–9 years and reach sizes up to 1 m in length (M. Román, unpublished data). According to local fishermen, *C. othonopterus* spawn in large aggregations between February and April both in the mouth of the Colorado River and some unknown distance upstream (Fig. 2). The fishing season corresponds with the annual spawning event.

We use oxygen isotope ratios in the otoliths of the *C. othonopterus* to evaluate the importance of Colorado River water to this fish's early life history. The saggital otoliths of *C. othonopterus* have distinct annual layers of aragonite ($CaCO_3$), which act as natural archives of environmental

© 2005 NRC Canada

Fig. 2. Colorado River mouth and upper Gulf of California with the estimated extent of the original Colorado River Estuary according to Lavín and Sánchez (1999) and Carbajal et al. (1997).



conditions. Fish otoliths have been used in many studies to determine age and as chemical logs for tracing migration (e.g., Stevenson and Campana 1992; Secor et al. 1995). Studies have shown that stable isotope signatures provide clear markers of behavior and habitat use, indicating whether fish inhabit marine, estuarine, or freshwater habitats (Dufour et al. 1992; Meyer-Rochow et al. 1992).

Our major objective is to use oxygen isotope ratios in otolith carbonate to test the hypothesis that *C. othonopterus* uses brackish-water habitat during early development. In this paper, we (*i*) demonstrate that growth increments in otoliths of *C. othonopterus* are annual, (*ii*) describe the observed otolith oxygen isotope profile throughout the fish's life, (*iii*) model the expected otolith oxygen isotope profile in the absence of Colorado River water for comparison with the observed values, (*iv*) determine if these fish spent their early development in brackish water created by the Colorado River, (*v*) determine the relationship between river flow and natal otolith $\delta^{18}O$ values, and (*vi*) calculate a range of salinities in which the natal otoliths developed.

Oxygen isotopes

The oxygen isotope ratio (or $\delta^{18}O$) of otolith aragonite is primarily controlled by the temperature and oxygen isotope ratio of the water in which the fish lived (Kalish 1991*a*; Thorrold et al. 1997; Weidman and Millner 2000). In the marine setting, where the $\delta^{18}O$ of seawater is relatively constant, oxygen isotope ratios in otoliths have a simple annual temperature-driven cycle through time, with the more negative $\delta^{18}O$ values associated with summer warmth and the more positive values associated with cooler temperatures (Patterson 1998; Weidman and Millner 2000; Andrus et al.

© 2005 NRC Canada

2002). As temperature increases, the $\delta^{18}O$ of biogenic carbonate decreases: for every 5 °C increase in temperature, the $\delta^{18}O$ decreases by approximately 1‰ (Weidman and Millner 2000). If a fish is restricted to fully marine conditions throughout its life, the $\delta^{18}O$ cycle in the otolith will remain within limits controlled by the temperature cycle. Otoliths from fish inhabiting water with a different isotopic composition, such as brackish estuarine habitats, will still have a temperature-driven cycle in the otolith $\delta^{18}O$, but the values will be more negative than a typical marine record because of the addition of isotopically negative river water to the estuary (Ingram et al. 1996; Dettman et al. 2004). In the case at hand, Colorado River water has a value of −12‰, in contrast to the +0.6‰ of the fully marine water of the upper Gulf of California (Dettman et al. 2004).

These two environmental controls (temperature and $\delta^{18}O$ of the water) of $\delta^{18}O$ variation in otoliths provide two ways in which the oxygen isotope record of an otolith can be used to document movement of fish between marine and estuarine waters. The first is identified as an excursion in the $\delta^{18}O$ record to values beyond the cycle created by seasonal temperature change. Negative $\delta^{18}O$ values beyond temperature-driven values clearly indicate a change in the $\delta^{18}O$ and are observed when there is a shift into estuarine conditions, because river waters are more negative in $\delta^{18}O$ than seawater (e.g., Fritz 1981; Ingram et al. 1996). The second way in which significant changes in the $\delta^{18}O$ of waters can be detected makes use of the relationship between temperature, the $\delta^{18}O$ of water, and the $\delta^{18}O$ of otolith aragonite (e.g., Thorrold et al. 1997). If a known temperature can be matched to a portion of the otolith where time of development is known, then the $\delta^{18}O$ of the water in which the fish lived can be calculated, distinguishing which isotopically distinct body of water the fish lived in during that time interval of otolith development. This paper will make use of both approaches to determine if *C. othonopterus* uses brackish water habitats in the Colorado River Estuary during its early development.

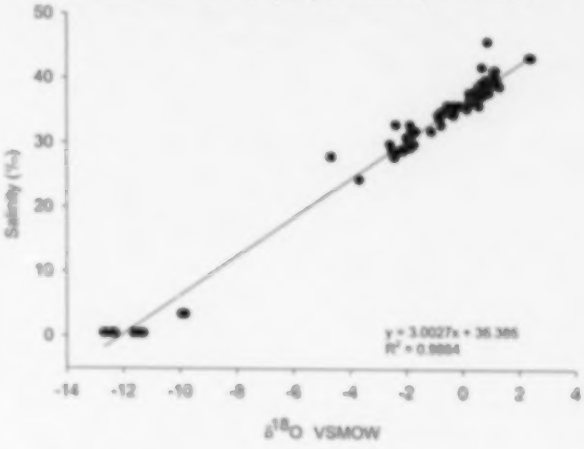
The linear relationship between salinity and $\delta^{18}O$ of water is well documented (Witbaard et al. 1994; Ingram et al. 1996; Elsdon and Gillanders 2002). This occurs because both the salinity and the oxygen isotope ratio are conservative properties. When mixing two waters of different salinities, the result is a simple proportional sum of the salinities. The oxygen isotope ratio of water derived from a mixture of two waters (A and B) is calculated the same way using an equation of the form

$$(1) \qquad \delta^{18}O_{mixture} = x\delta^{18}O_A + (1 - x)\delta^{18}O_B$$

where x is the decimal fraction of A in the mixture.

The salinity in which the fish lived can be derived from the calculated $\delta^{18}O$ of water inhabited by *C. othonopterus* at a known time, because the relationship between salinity and $\delta^{18}O$ value of upper Gulf of California and lower Colorado River water have been monitored during the last 10 years (Dettman et al. 2004). The water in the Colorado River Estuary is a simple mixture of these two end members, leading to the linear relationship shown in Fig. 3. The relationship between $\delta^{18}O$ values and salinity thus allows us to reconstruct habitat salinity from otolith chemistry, and in this way, the annually banded otoliths can serve as biotic "flight recorders" of the environmental conditions experienced during the life of the individual fish.

Fig. 3. Linear relationship between salinity and $\delta^{18}O$ values of waters (relative to Vienna Standard Mean Ocean Water (VSMOW)) in the lower Colorado River and the Colorado River Estuary over the past decade ($r^2 = 0.9864$, $F_{[1,137]} = 9947.98$, $p < 0.0001$).



Methods

Study area

The Colorado River Estuary is at the terminus of the 2800 km long Colorado River and once extended 70 km south into the upper Gulf of California (Fig. 2) (Lavín and Sánchez 1999). The Colorado River watershed drains approximately 391 000 km^2 of southwestern North America, and before upstream diversions and impoundments, annual river flow into the Gulf of California ranged from 8×10^9 to 30.8×10^9 m^3·year^{-1} (Harding et al. 1995) (Fig. 1). Most of the river's flow is derived from snowmelt from the western slope of the Rocky Mountains. Before the dams, snowmelt delivered as much as 75% of the river's annual flow to the estuary during the months of May, June, and July (Harding et al. 1995; Lavín and Sánchez 1999). The Colorado River once created 4000 km^2 of brackish-water habitat in the upper Gulf of California (Carbajal et al. 1997; Lavín and Sánchez 1999; Rodriguez et al. 2001*b*) and was also a major source of sediments for the Colorado River Delta (Alvarez and Jones 2002) and nutrients to the upper Gulf of California. Since about 1960, the Colorado River has rarely reached the Gulf (Hernández-Ayón et al. 1993; Lavín and Sánchez 1999).

The Colorado River Estuary is now a negative estuary: salinity decreases toward the open Gulf (Bray 1988; Lavín et al. 1998; Alvarez and Jones 2002). High evaporation rates and decreased river flow have resulted in salinities between 36‰ and 42‰ (averaging 38‰) in the upper Gulf (Hernández-Ayón et al. 1993; Lavín and Sánchez 1999; Calderon-Aguilera et al. 2003). The estuary is shallow (1–40 m), with a tidal range of up to 10 m (Carbajal et al. 1997; Lavín and Sánchez 1999). Strong tidal currents resuspend the muddy sediments of the delta, resulting in a well-mixed and turbid estuary (Hernández-Ayón et al. 1993). Water temperature can range from ~8 to ~31 °C during the year (Lavín et al. 1998).

© 2005 NRC Canada

Sampling

We sampled otoliths from 18 *C. othonopterus* purchased in markets in El Golfo de Santa Clara, Sonora, Mexico (Fig. 2), in 1997, 1998, 2000, 2001, and 2002. Fish were caught in the mouth of the Colorado River Estuary. Methods for retrieving, mounting, and sampling sagittal otoliths are well established for investigating age and environmental conditions (e.g., Stevenson and Campana 1992; Secor et al. 1995). Sagittal otoliths were cleaned ultrasonically in distilled water and cut dorso-ventrally into 1 mm sections by using an Isomet low-speed saw equipped with a diamond blade. Otolith sections were mounted on glass slides and polished using 0.05 µm grit. Polished sections were photographed under reflected light, and growth increments were counted from digital images.

Oxygen isotopes

We made isotopic profiles of four otoliths by sampling along a transect from the perimeter (terminal year) to the core (natal otolith) using a micromill drill with a 0.3 mm drill bit. By shaving off portions of increments with a micromill (Dettman and Lohmann 1995), the samples provide a high-resolution account of isotopic variation during the life of the fish. In addition, we sampled the core (natal portion) of the saggital otolith of 14 individuals to test our hypothesis that these fish lived in brackish water provided by the Colorado River flows during early development. All samples weighed between 30 and 60 µg. The samples were heated to 180 °C in a vacuum oven for 1 h to remove volatile material. Oxygen isotope ratios in carbonates are expressed relative to the Vienna Pee Dee Belemnite (VPDB) standard. Otolith carbonate was analyzed at the Stable Isotope Laboratory of the Department of Geosciences, University of Arizona, using a Finnigan MAT 252 mass spectrometer (Thermo Electron Corp., Waltham, Mass.) equipped with a Kiel-III automated carbonate sampling device (Thermo Electron Corp.). Standardization of oxygen isotope ratios was based on normalization to published ratios of NBS19 and NBS18. Analytical error was ±0.1‰.

Temperature-driven variation in oxygen isotopes

We modeled the expected temperature-driven variation in $\delta^{18}O$ of otolith carbonate by using the corrected Thorrold et al. (1997) equation by Weidman and Millner (2000). The oxygen isotope fractionation equation relating temperature and the average $\delta^{18}O$ value of the upper Gulf of California to otolith carbonate is

$$(2) \qquad \delta^{18}O_{\text{expected otolith}} = 4.38 - 0.21T + \delta^{18}O_{\text{water}}$$

where T represents temperature (°C). $\delta^{18}O_{\text{expected otolith}}$ is expressed relative to VPDB (‰), and $\delta^{18}O_{\text{water}}$ is expressed relative to Vienna Standard Mean Ocean Water (VSMOW; ‰). We used monthly averages of surface-water temperature from Puerto Peñasco, Sonora, Mexico, based on a 38-year record (1964–2002) of daily temperatures (P. Turk-Boyer, Intercultural Center for the Study of Deserts and Oceans, P.O. Box 44208, Tucson, AZ 85341, USA (peggy@cedointercultural.org), personal communication, 2004). The average $\delta^{18}O$ of northern Gulf of California water over the last decade is 0.6‰ VSMOW during times when there was no inflow of Colorado River water (Goodwin et al. 2002; Dettman et al. 2004).

We use the relationship between temperature, water $\delta^{18}O$, and otolith $\delta^{18}O$ established by Thorrold et al. (1997). This relationship is experimentally derived and is the only estimate based on a sciaenid, the Atlantic croaker (*Micropogonias undulatus*). Because large differences in physiology and life history between species may affect the relationship between temperature and fractionation (Weidman and Millner 2000; Høie et al. 2004), picking an equation based on a closely related fish is important. *Cynoscion othonopterus* is more similar in life history, behavior, and habitat preferences to *M. undulatus* than to fish used in other studies (e.g., Kalish 1991*a* (salmonid); Weidman and Millner 2000 (cod); or Høie et al. 2004 (cod)). Furthermore, the temperature and salinity conditions used in the experiments of Thorrold et al. (1997) are similar to those experienced by *C. othonopterus* in the wild.

It should be pointed out that because our temperature-driven model assumes a constant rate of growth, we are not comparing the shape of the $\delta^{18}O$ profile. Instead, we are only interested in the range of expected values. Because of periods of slow or no growth in the otolith, not all of the expected values may occur in the observed otolith $\delta^{18}O$ record; however, all observed values should occur in the model if the fish inhabited only marine water.

Colorado River influence on isotopic composition

We compared the modeled temperature-driven variation in $\delta^{18}O$ with the observed $\delta^{18}O$ variation in the otolith samples. The $\delta^{18}O$ values that are lower than those predicted by the hottest temperatures during the year indicate the influence of Colorado River water.

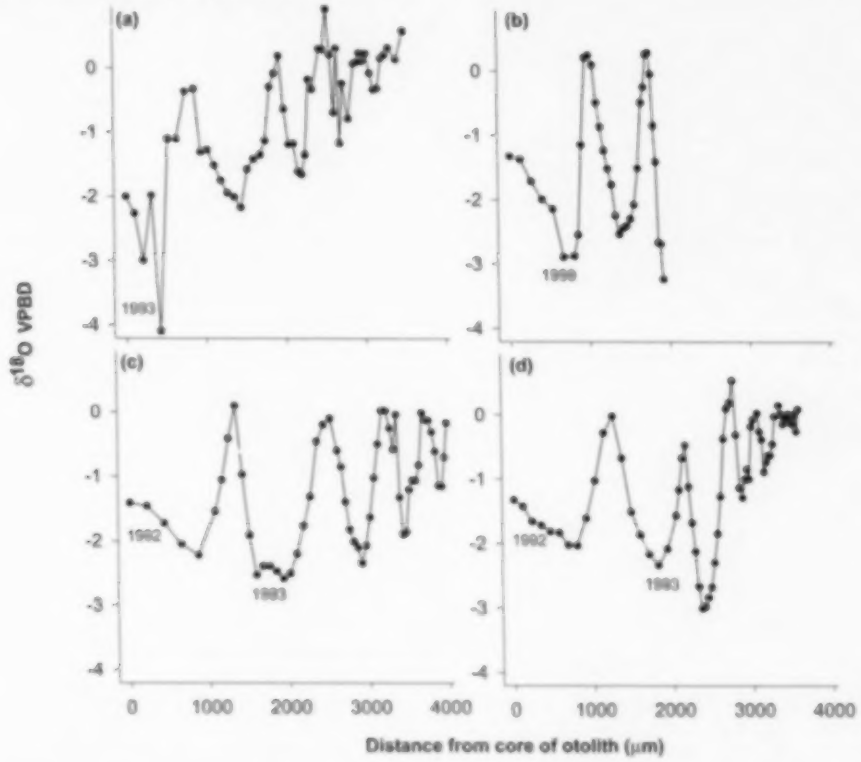
We also compared observed values in the natal region of the otolith with values predicted by the temperature-driven model. We used two predicted $\delta^{18}O$ values: one based on the average temperature during the three-month period (February to April) of early development for the specific year represented by the natal portion of each otolith and the other based on the warmest daily temperature recorded during that period for that year of birth. Although it is unlikely that the natal portion of the otolith formed on the hottest day of that period, we use this as a conservative estimate, because using the highest possible temperature produces the most negative $\delta^{18}O$ value. We determined the year of birth by counting growth increments back from the date of collection. The expected values were compared with the observed otolith $\delta^{18}O$ values for each natal portion using a paired t test.

If the observed natal $\delta^{18}O$ values are significantly less than those predicted by our temperature-driven model, we conclude that the natal portion of the otolith was developed while the fish was in waters mixed with isotopically negative Colorado River water. Because both high temperature and the influx of −12‰ (VSMOW) Colorado River water result in low $\delta^{18}O$ values in the otolith, natal $\delta^{18}O$ values lower than those that could be produced by temperature on the hottest day are unequivocal indicators of the influence of the Colorado River water.

If $\delta^{18}O$ values observed in the natal otolith are attributed to the influence of the Colorado River water, there should be

© 2005 NRC Canada

Fig. 4. The $\delta^{18}O$ variation in otoliths from four *C. othonopterus* caught in different years, where $\delta^{18}O$ is relative to Vienna Pee Dee Belemnite (VPDB). The *x* axis measures distance from the natal (core) portion of the otolith to the time of death (perimeter). Years of unusually high river flow (1993) and birth year are labeled.



a relationship between the $\delta^{18}O$ values and the volume of Colorado River water flowing into the upper Gulf of California. We used log-linear regression to evaluate the relationship between natal $\delta^{18}O$ and total river flow volume during the months of natal otolith growth (February through April).

Salinity

We use the isotopic composition of the natal otolith to calculate salinity by first calculating the $\delta^{18}O$ of the natal habitat water and then using the relationship shown in Fig. 3 to convert the $\delta^{18}O$ of water in this mixing zone to salinity. This calculation takes advantage of the fact that otolith carbonate is precipitated in equilibrium with the ambient water (Kalish 1991*b*; Thorrold et al. 1997; Weidman and Millner 2000). Again, we used two temperatures to calculate the water $\delta^{18}O$ value, the average temperature of the natal period (February to April of the year of birth) and the warmest temperature recorded during that period. We back-calculated the $\delta^{18}O$ of the water from the observed $\delta^{18}O$ of natal otoliths using these temperatures and eq. 2. We then used the linear mixing relationship between local seawater ($\delta^{18}O$ = +0.6‰ VSMOW, salinity = 38‰) and Colorado River water ($\delta^{18}O$ = –12.0‰ VSMOW, salinity = 0‰) to calculate the salinity for a given mixed-water $\delta^{18}O$ value. These end members (Fig. 3) and eq. 1 result in the following relationship for the modern Colorado River Estuary zone:

$$\text{salinity (‰)} = 36.4 + 3.0(\delta^{18}O_{water})$$

Results

Observed isotopic profile

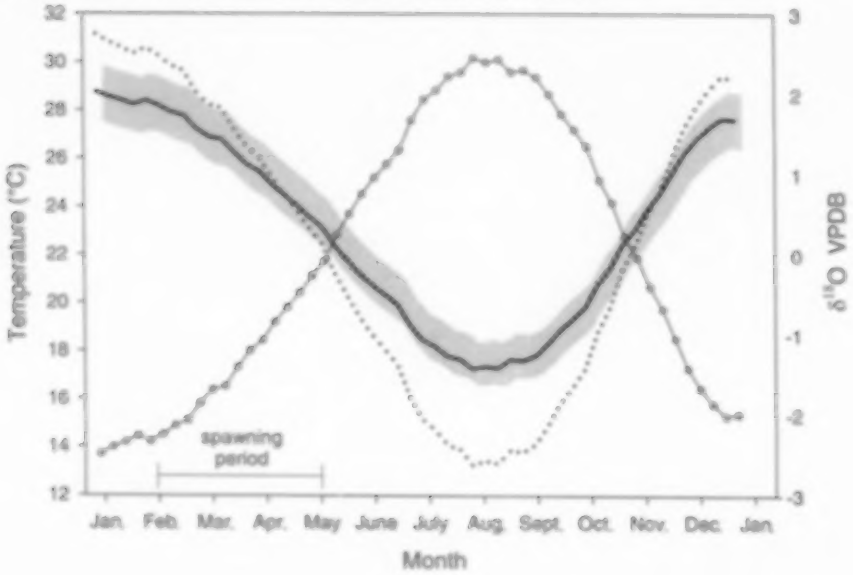
The $\delta^{18}O$ values from *C. othonopterus* otoliths show distinct cycles from the natal core to the perimeter, similar to those in other oxygen isotope studies of otoliths (Patterson 1998; Weidman and Millner 2000; Andrus et al. 2002). Maximum $\delta^{18}O$ values occur in opaque zones and minimum $\delta^{18}O$ values occur in translucent zones. The $\delta^{18}O$ values range from a maximum of +0.99‰ to a minimum of –4.09‰ VPDB. The $\delta^{18}O$ values in the natal part of the otoliths range from a maximum of –0.39‰ to a minimum of –2.73‰ VPDB. The range of $\delta^{18}O$ values is greatest during the first two cycles (bands). After the second or third band, the isotopic variation decreases to ~2‰. The three otoliths taken from older fish showed similar isotopic cycles with progressively reduced variation toward the perimeter of the otolith (Figs. 4*a*–4*d*).

Temperature effects

Expected temperature-driven annual variation in $\delta^{18}O$ values for a fish growing throughout a year has a range of almost 3.44‰, using the adjusted Thorrold et al. (1997) equation (eq. 2). For fish growing in the absence of river in-

© 2005 NRC Canada

Fig. 5. The relationship between upper Gulf of California surface water temperatures and $\delta^{18}O$ values in otoliths. Shaded circles represent weekly averages of temperature from 1964–2003 at Puerto Peñasco, Sonora, Mexico (P. Turk-Boyer, Intercultural Center for the Study of Deserts and Oceans, P.O. Box 44208, Tucson, AZ 85341, USA (peggy@cedointercultural.org), personal communication, 2003). Shaded range is the annual temperature-driven variation of $\delta^{18}O$ values predicted by the following published equations: Grossman and Ku (1986); Thorrold et al. (1997); Weidman and Millner (2000); Radtke et al. (1998); Høie et al. (2004). The solid line is the seasonal variation of $\delta^{18}O$ predicted by this study (eq. 2) based on the study of Thorrold et al. (1997), and the dotted line is the range predicted by Kalish (1991*a*). These modeled $\delta^{18}O$ profiles are based on the surface water temperatures and a $\delta^{18}O$ value for Gulf of California water of 0.6‰ relative to Vienna Standard Mean Ocean Water (VSMOW).



flux, the expected maximum winter value is +2.10‰ and the minimum summer value is –1.36‰. This range is comparable to those published by Grossman and Ku (1986), Thorrold et al. (1997), Weidman and Millner (2000), Radtke et al. (1998), and Høie et al. (2004) and markedly different from that of Kalish (1991*a*) (Fig. 5).

Observed otolith $\delta^{18}O$ values differed from the predicted annual temperature-driven variation in four ways (Figs. 4*a*–4*d*). (*i*) The otoliths lack $\delta^{18}O$ values from the coldest months. The most positive value observed in the otoliths is +0.99‰, which is considerably lower than the expected winter value of +2.10‰. (*ii*) The otoliths do not always possess $\delta^{18}O$ values from the warmest months, especially in the later years of life. The minimum value tends to become more positive with age. (*iii*) Otolith values are more negative than the expected summer values, if driven by temperature alone, in the first two growth increments. (*iv*) The observed natal otolith $\delta^{18}O$ values are more negative than the predicted $\delta^{18}O$ values (+1.45‰ to –0.38‰), which use water temperatures for the upper Gulf of California during the period of early development (14 °C and 24 °C). The most negative value during the first two growth increments is –4.09‰ (Fig. 4*a*) and for the later years is –3.23‰ (Fig. 4*d*).

Colorado River influence on isotopic composition

Observed natal otoliths $\delta^{18}O$ values are between –0.39‰ and –2.73‰, which is significantly lower ($p < 0.0001$, df = 17, mean difference = –2.65) than the expected temperature-driven values, documenting the presence of isotopically negative water. Even if these fish were from a late spawn and the natal otolith was formed during the hottest day of April for the year of birth, observed natal $\delta^{18}O$ values in *C. othonopterus* are still significantly more negative ($p < 0.0001$, df = 17, mean difference = –1.35) than the values predicted by the model. These differences are greater for otoliths developed during years of high flow than in otoliths precipitated during years of low flow (Figs. 6*a*–6*b*).

We also found a significant log-linear relationship between natal otolith $\delta^{18}O$ values and the cumulative river flow volume during the February to April spawning season ($r^2 = 0.342$, $F_{[1,16]} = 9.854$, $p = 0.0063$), indicating greater use of brackish water in years when more Colorado River water reached the Gulf. This relationship is strongest using the cumulative flows for only the beginning of the spawning season (February) ($r^2 = 0.505$, $F_{[1,16]} = 18.357$, $p = 0.0006$) (Fig. 7).

Salinity

The salinity recorded in the natal otoliths of *C. othonopterus* nursery habitat varies depending on the cohort year and if the average or maximum surface temperature was used in the model. If we use that year's average temperature during time of early development, we estimate salinities between 26.4‰ and 34‰ (average = 30.2‰) (Table 1). If we assume that these fish were from a late spawn and developed during the warmest day of that year's spawning season, salinities would be between 29.6‰ and 37.8‰ (average = 34.2‰). Today the upper Gulf of California has an average

© 2005 NRC Canada

Fig. 6. Observed and expected $\delta^{18}O$ values (relative to Vienna Pee Dee Belemnite, VPDB) for the natal portion of *C. othonopterus* otoliths ($n = 18$). Expected values are calculated using eq. 2 and either the average temperature in February through April or the hottest temperature observed in April during the year of hatching. The observed values for the natal otolith are significantly lower ($p = 0.0001$) than values explained by temperature alone. (*a*) Observed and expected natal $\delta^{18}O$ values for fish born during years of low river flow conditions (flows < 100×10^6 m^3 in excess of the 1944 Mexican Water Treaty) (1992, squares; 1994, triangles; 1995, circles). (*b*) Natal values for fish born during years of high river flow (flows > 100×10^6 m^3 in excess of the 1944 Mexican Water Treaty) (1993, squares; 1997, circles; 1999, triangles).

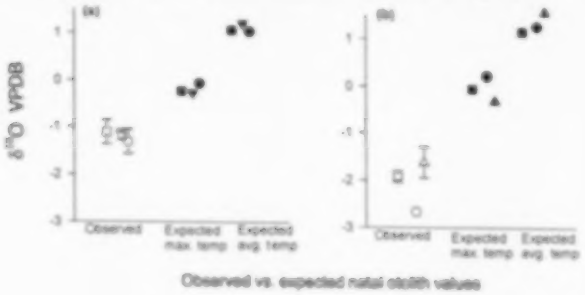
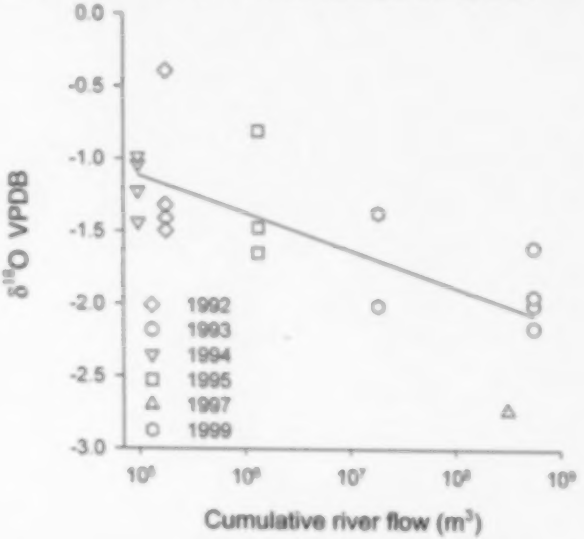


Fig. 7. Relationship between *C. othonopterus* natal otolith $\delta^{18}O$ values (relative to Vienna Pee Dee Belemnite (VPDB)) and the cumulative Colorado River flow for the month of February (beginning of spawning season) for that year of early development ($r^2 = 0.505$, $F_{[1,16]} = 18.357$, $p = 0.0006$). The *x* axis is a log scale.



salinity of 38‰ (Hernández-Ayón et al. 1993; Lavín and Sánchez 1999). Isotopically based estimates of salinity during the natal growth are from ~0.2‰ to 11.6‰ less than salinities typical of upper Gulf of California water.

Discussion

Isotopic profile

The oxygen isotopic record in the saggital otoliths of *C. othonopterus* displays a seasonal, temperature-driven pattern of variation demonstrating that growth increments are annual. Opaque zones (when viewed in reflected light) form in winter, and translucent zones form during the summer. The banding patterns reported here, showing associations between seasonal temperature variation and growth banding, are well documented in otoliths (Kalish 1991*b*; Weidman and Millner 2000; Campana and Thorrold 2001).

Many of the differences between expected and observed annual $\delta^{18}O$ otolith profiles are concentrated at the temperature-driven extreme values (coldest and warmest). The missing extreme values in the otolith profiles can be explained by seasonal and interannual differences in growth rates. Growth rates in fish are primarily influenced by temperature and life history stage such that growth slows at extreme temperatures and with increasing age (Otterlei et al. 2002). Both temperature extremes and ontogeny are likely to affect growth in *C. othonopterus*. Periods of slow or no growth, regardless of the cause, result in either a reduced isotopic resolution (because of the missing record resulting from no growth) or the mixing of $\delta^{18}O$ values from more than one thin lamina in the slow-growth portions of the otolith (see Goodwin et al. (2002) for a discussion of these effects in accretionary hard parts). Note that in both cases, the isotopic record will fail to capture the extreme values of the annual cycle.

The most positive values predicted for the winter months do not occur in *C. othonopterus* otoliths. The average maximum otolith $\delta^{18}O$ value is 0.46‰. Values higher than this are rare, which suggests that these fish do not grow or grow very slowly during the coldest time of year. If their otoliths continue growing during these cold temperatures, the amount of material deposited is so little that the minimum $\delta^{18}O$ values are mixed with adjacent higher values in our samples.

Temperature-induced growth checks are common among temperate fish (Panella 1980). For example, Wurster and Patterson (2001) found that the isotopic record of *Aplodinotus grunniens* otoliths indicate a cessation of growth when temperatures are below 10 °C. Several studies have also found that temperature is one of the most influential environmental factors determining growth in several species of *Cynoscion* (Lankford and Targett 1994; Paperno et al. 2000).

An alternative explanation for the lack of colder temperatures recorded in the otolith carbonate is that the fish move to thermal refugia during winter months. This is unlikely, as such refugia would require thermal stratification of upper Gulf water, a feature that is not present in these shallow waters because of the strong tidal mixing (Hernández-Ayón et al. 1993). Because these fish are restricted to the northern Gulf of California, migration south to warmer waters is not a plausible explanation. We consider slow growth during winter temperatures a plausible explanation for the absence of extreme winter values.

Summer minimum $\delta^{18}O$ values in the otoliths vary depending on the age of the fish and the environmental conditions of the particular year. The rapid growth in the first and second year (especially during summers) provides high temporal resolution and therefore captures the warm summer temperatures of the upper Gulf of California. All fish have minimum values for the first year that are lower than would

© 2005 NRC Canada

Table 1. *Cynoscion othonopterus* year of birth, $\delta^{18}O$ values for natal otolith, mean water temperature (mean temp.) and maximum water temperature (max. temp.) recorded for year of birth between February and April, salinity calculated using mean temperature (mean salinity) and maximum temperature (max. salinity), and total Colorado River flow from Yuma gage for February of year of birth.

Sample ID	Year spawned	Natal $\delta^{18}O$, ‰	Mean temp., °C	Max. temp., °C	Mean salinity, ‰	Max. salinity, ‰	February river flow, m^3
Co 1	1992	–1.32	18.9	25	31.2	35.1	1.8×10^5
Co 2	1992	–1.41	18.9	25	30.9	34.8	1.8×10^5
Co 3	1992	–0.39	18.9	25	34	37.8	1.8×10^5
Co 4	1992	–1.49	18.9	25	30.7	34.5	1.8×10^5
Co 5	1993	–2.00	18.2	24	28.8	32.4	5.6×10^8
Co 6	1993	–2.16	18.2	24	28.3	31.9	5.6×10^8
Co 7	1993	–1.94	18.2	24	28.9	32.6	5.6×10^8
Co 8	1993	–1.60	18.2	24	30	33.6	5.6×10^8
Co 9	1994	–1.44	18	25	30.3	34.7	9.6×10^4
Co 10	1994	–1.04	18	25	31.5	35.9	9.6×10^4
Co 11	1994	–0.99	18	25	31.6	36	9.6×10^4
Co 12	1994	–1.23	18	25	30.9	35.3	9.6×10^4
Co 13	1995	–0.80	18.8	24	32.7	36	1.3×10^6
Co 14	1995	–1.65	18.8	24	30.2	33.4	1.3×10^6
Co 15	1995	–1.47	18.8	24	30.7	34	1.3×10^6
Co 16	1997	–2.73	18	23	26.4	29.6	3.1×10^8
Co 17	1999	–1.37	16.8	25.5	29.7	35.2	1.8×10^7
Co 18	1999	–2.01	16.8	25.5	27.8	33.3	1.8×10^7

be expected if temperature was the only influence on the $\delta^{18}O$ values. The summer $\delta^{18}O$ values after the second year of growth are progressively more positive, which suggests that growth slows with increasing age, reducing sample resolution. A similar pattern of attenuation of annual $\delta^{18}O$ variation has been documented in other otoliths (Gao and Beamish 1999; Andrus et al. 2002; Weidman and Millner 2000). Gao and Beamish (1999) suggested that this pattern of increasing minimum $\delta^{18}O$ with age in sockeye salmon (*Oncorhynchus nerka*) was the result of a shift in habitats. The progressive nature of the increase in summer values in Gulf corvina otoliths, however, supports the explanation that growth progressively slows with increasing age during the warmest part of the year. This is more likely the mechanism behind the progressive increase in the annual minimum $\delta^{18}O$ values, based on the decreasing widths of the growth increments sampled and the fact that Gulf corvina are endemic to the Gulf of California.

Colorado River influence on the isotopic composition

The most provocative differences between the observed $\delta^{18}O$ record and the expected values are those that cannot be explained by temperature. These anomalies occur during the spring and summer seasons of the first two years, when otoliths grow rapidly and provide a detailed record. Maximum water temperatures for summers are ~31 °C, yielding a predicted $\delta^{18}O$ value of –1.4‰. These departures from the expected summer $\delta^{18}O$ values are greatest for the fish spawned during high release years. We observe values as low as –4.09‰, which yields an estimated water salinity of 30‰ if this part of the otolith developed during the warmest part of the summer. These negative anomalies occur during years of excess Colorado River flow (1993 and 1999) and are unequivocally the result of these fish using habitat that is influenced by influx of river water. The two otoliths in Figs. 4*c* and 4*d* have $\delta^{18}O$ values in the first summer that are also more negative than expected, even though it is a low-flow year. While river flows in excess of the Mexican Water Treaty were low during 1992 summer (May–August), at least 37 million m^3 of water (above treaty requirements) were released, and this water likely affected these summer $\delta^{18}O$ values. The negative values during the first year of growth in high- and low-flow years document growth in brackish water, supporting our hypothesis that Gulf corvina inhabit the less saline waters of the Colorado River Estuary during their early life history.

The $\delta^{18}O$ values of the natal otolith also demonstrate that their earliest days of life took place in brackish water. Even if these fish formed the natal portion of their otoliths on the warmest day of that year's spawning season, the minimum $\delta^{18}O$ values are significantly more negative than such temperatures predict. Similarly, the natal values are significantly more negative if based on equations such as those of Kalish (1991*a*) ($p < 0.0001$, df = 17, mean difference = –0.79), which has a steeper slope and would result in more negative predicted values.

The negative correlation between river volume and natal $\delta^{18}O$ values provides additional evidence that the otoliths record the presence of Colorado River water. The correlation also suggests that these fish are not passively recording the river's flow. If this were the case, we would expect to see a linear relationship between flow and the observed natal $\delta^{18}O$ values, where a proportional change in water would result in the same proportional change in $\delta^{18}O$ values. Instead, a log-linear relationship between river flow and $\delta^{18}O$ values provides a better fit to the data, suggesting a preferred salinity. Gulf corvina may behaviorally regulate the salinity they experience. They may select particular salinities and not move into increasingly freshwater habitat as more Colorado River water is delivered. Such preferences are consistent with

© 2005 NRC Canada

sciaenid biology (Chao 1978; Blaber 1997; Fennessy 2000) and have been documented in the genus *Cynoscion* (Matlock 1987; Lankford and Targett 1994; Baltz et al. 1998). Sciaenids use brackish waters for spawning and nursery sites, but they are not anadromous fish.

The genus *Cynoscion* is comprised of marine and estuarine species and, like other sciaenids, is known to primarily use estuaries for spawning and nursery grounds (Chao 1978; Blaber 1997; Fennessy 2000). We document that *C. othonopterus* from years of low flow, as well as those from years of large flows, have natal $\delta^{18}O$ values that are more negative than expected. This suggests that larval *C. othonopterus* actively seek microhabitats that are less saline, when available, even during years of little river inflow. Such microhabitats may provide larval and juvenile fish with the appropriate environmental conditions to enhance their growth and survival. Studies of congeners indicate that the rate of growth during early development increases as salinity decreases (Matlock 1987; Baltz et al. 1998; Kucera et al. 2002). Indeed, Baltz et al. (1998) found that moderate salinities contribute more to *Cynoscion nebulosus* growth than diet or other extrinsic factors. Additionally, 20‰ is documented to be the optimal salinity for *Cynoscion regalis* growth during summer temperatures (Lankford and Targett 1994).

The freshwater plume of the Colorado River can extend as far as 70 km into the Gulf of California when river flows are high (Carbajal et al. 1997; Rodriguez et al. 2001*b*) and recedes during low-flow years. Because the area of suitable nursery grounds for *C. othonopterus* would increase with increased Colorado River flow and other species of *Cynoscion* grow more rapidly in lowered salinity, the population of this commercially important fish would likely benefit from increased river flow. The significant increase in catch in the years following the 1993 release of excess waters supports this idea. Salinities in the freshwater plume of the Colorado River during the 1993 controlled release of river water ranged from 26‰ to 36‰ and extended at least 70 km south of the mouth of the river (Lavín and Sanchez 1999), providing an enlarged nursery area for *C. othonopterus*. In addition, modeled salinities of the upper Gulf during steady Colorado River flows resulted in salinities of 26‰ extending down to San Felipe (Carbajal et al. 1997). The salinity calculated for the natal otoliths of fish spawned during that flood event averaged 28.9‰, almost 10‰ lower than average post-dam salinities in the upper Gulf of California. This suggests that these fish were spawned and began development within the freshwater plume in the upper Gulf of California.

Where do the larval fish go during years when little to no Colorado River flow was available? It is possible that indirect inflow sustains some nursery habitat. Although surface freshwater inflow has been scarce in the last 40 years, groundwater input to the estuary may provide brackish microhabitats (Hernández-Ayón et al. 1993). Hernández-Ayón et al. (1993) suggest that agricultural return flow percolates through the sediments of the Colorado River Delta and is a likely source of fresh water that flows into the Gulf of California. In addition, Lavín et al. (1998) conclude that the delivery of subsurface Colorado River water from upstream agriculture during years of no surface flow contributes to increased nutrients in the upper Gulf. Such groundwater flow may emerge from submarine springs and provide brackish habitats for juvenile fish even during years of no surface flow.

Implications

Our results confirm that the Colorado River Estuary functions as essential nursery grounds for the upper Gulf of California. Other studies also provide empirical evidence that Colorado River flow is important to the biota of its estuary and the northern Gulf of California. For example, river flow is positively correlated with postlarval shrimp abundance in the estuary (Aragón-Noriega and Calderon-Aguilera 2000) and shrimp catches in the northern Gulf; Galindo-Bect et al. (2000) calculate that an increase of only 30.8×10^7 $m^3 \cdot year^{-1}$ of Colorado River water could double shrimp production in the upper Gulf (shrimp are also one item of the *C. othonopterus* diet). The decline in the population of the bivalve mollusk *Mulinia coloradoensis* is attributed to the decline in river flow (Kowalewski et al. 2000; Rodriguez et al. 2001*a*), and this species' decline may have led to the decline of its predators (Cintra-Buenrostro et al. 2005). In addition, Glenn et al. (1996) estimate that returning only 0.5% of mean annual flow could sustain the lush riparian and aquatic habitats in the terrestrial portion of the Colorado Delta (see also Pitt et al. 2000; Glenn et al. 2001). Our results show that we can now add *C. othonopterus* to the list of species that would benefit from increased flow. Restoration and management of the Gulf corvina fishery require additional river water for the fish's nursery habitats, as well as regulation of fishing practices.

The importance of freshwater flow to estuaries and fisheries has been well documented in other settings. For example, approximately 60% of fish landed by the American fishing industries spend part of their life in estuaries (Owen and Chiras 1995). In the Louisiana estuaries, 90% of the fishes use the estuarine habitat for nursery grounds (see references in Blaber 1997). Extensive research on Texas bays and estuaries has documented the value of freshwater inflows to commercial fisheries there and has justified standards for minimum flows (Longley 1994; Powell et al. 2002). Although rivers have often been managed as discrete habitats that have no effects on adjacent and estuarine habitats, the consequences of doing so can be harmful to the environment, economy, and society (Wilber 1992; Drinkwater and Frank 1994; Grimes and Kingsford 1996).

In conclusion, oxygen isotopes in the natal portions of otoliths of *C. othonopterus* demonstrate that this species' initial growth occurs in brackish-water habitats created by inflow of Colorado River water. After adjusting for the effects of temperature, $\delta^{18}O$ values indicate that the nursery grounds have salinities between 26‰ and 38‰. Successful restoration of the Gulf corvina fishery in the upper Gulf of California requires influx of Colorado River water to nursery grounds in the river's estuary.

Acknowledgements

We thank José Campoy for sharing his knowledge of the area and for being passionate about science-driven management of the Colorado River Delta and upper Gulf of California. We also thank Peggy Boyer for the use of temperature

© 2005 NRC Canada

data collected by the Intercultural Center for the Study of Deserts and Oceans (CEDO). Josh Tewksbury, Lloyd Findley, Peter Reinthal, Dean and Sandra Blinn, Linn Montgomery, David Goodwin, and Carlos Cintra-Buenrostro contributed to this paper through inspiring conversations. The comments of two anonymous reviewers helped strengthen this paper. This project was funded by grants from National Science Foundation to KWF and DLD and from T&E Inc. to KR, a Southern Arizona Environmental Management Scholarship to KR, National Science Foundation Dissertation Enhancement Grant to KR, and the Marshall Foundation Dissertation Fellowship to KR. This is Centro de Estudios de Almejas Muertas (CEAM) publication No. 51.

References

Andrus, C.F., Crowe, D.E., Sandweiss, D.H., Reitz, E.J., and Romanek, C.S. 2002. Otolith $\delta^{18}O$ record of mid-Holocene sea surface temperature in Peru. Science (Washington, D.C.), **295**: 1508–1511.

Alvarez, L.G., and Jones, S.E. 2002. Factors influencing suspended sediment flux in the upper Gulf of California. Estuar. Coast. Shelf Sci. **54**: 747–759.

Aragón-Noriega, E.A., and Calderon-Aguilera, L.E. 2000. Does damming the Colorado River affect the nursery area of blue shrimp *Litopenaeus stylirostris* (Decapods: Penaeidae) in the upper Gulf of California? Int. J. Trop. Biol. Conserv. **48**: 867–871.

Blaber, S.J.M. 1997. Fish and fisheries of tropical estuaries. *In* Fisheries Series. Vol. 22. Chapman Hall, New York. pp. 44, 111–138, 185–212, 215–221.

Baltz, D.M., Fleeger, J.W., Rakocinski, C.F., and McCall, J.N. 1998. Food density and microhabitat: factors affecting growth and recruitment potential of juvenile saltmarsh fishes. Environ. Biol. Fishes, **53**: 89–103.

Bray, N.A. 1988. Thermohaline circulation in the Gulf of California. J. Geophys. Res. **93**: 4993–5020.

Brusca, R.C., Findley, L.T., Hastings, P.A., Hendrick, M.E., Torre-Cosío, J., and van der Heiden, A.M. 2005. Macrofaunal biodiversity in the Gulf of California. Biodiversity in the Gulf of California (Sea of Cortez). *In* Biodiversity, ecosystems and conservation in Northern Mexico. *Edited by* J.L.E. Cartron and G. Ceballos. Oxford University Press, New York.

Calderon-Aguilera, L.E., Marinone, S.G., and Aragón-Noriega, E.A. 2003. Influence of oceanographic processes on the early life states of the blue shrimp (*Litopenaeus stylirostris*) in the Upper Gulf of California. J. Mar. Sys. **39**: 117–128.

Campana, S.E., and Thorrold, S.R. 2001. Otoliths, increments and elements: keys to a comprehensive understanding of fish populations. Can. J. Fish. Aquat. Sci. **58**: 30–38.

Carbajal, N., Souza, A., and Durazo, R. 1997. A numerical study of the ex-ROFI of the Colorado River. J. Mar. Sys. **12**: 17–33.

Chao, L.H. 1978. A basis for classifying western Atlantic Sciaenidae. NOAA Tech. Rep. NMFS Circ. **415**: 68.

Cintra-Buenrostro, C.E., Flessa, K.W., and Avila-Serrano, G., 2005. Who cares about a vanishing clam? Trophic importance of *Mulinia coloradoensis* inferred from predatory damage. Palaios, **20**: 295–301.

Cisneros-Mata, M.A., Montemayor-López, G., and Román-Rodríguez, M.J. 1995. Life history and conservation of *Totoaba macdonaldi*. Conserv. Biol. **9**: 806–814.

D'Agrosa, C., Lennert-Cody, C.E., and Vidal, O. 2000. Vaquita bycatch in Mexico's artisanal gillnet fisheries: driving a small population to extinction. Conserv. Biol. **14**: 1110–1119.

Dettman, D.L., and Lohmann, K.C. 1995. Approaches to microsampling carbonates for stable isotope and minor element analysis: physical separation of samples on a 20 micrometer scale. J. Sediment. Petrol. **A65**: 566–569.

Dettman, D., Flessa, K.W., Roopnarine, P.D., Schöne, B.R., and Goodwin, D.H. 2004. The use of oxygen isotope variation in shells of estuarine mollusks as a quantitative record of seasonal and annual Colorado River discharged. Geochim. Cosmochim. Acta, **68**: 1253–1263.

Drinkwater, K.F., and Frank, K.T. 1994. Effects of river regulation and diversion on marine fish and invertebrates. Aquat. Conserv. Freshwater Mar. Ecosyst. **4**: 135–151.

Dufour, V., Pierre, C., and Rancher, J. 1992. Stable isotopes in fish otoliths discriminate between lagoonal and oceanic residents of Taiaro Atoll (Tuamotu Archipelago French Polynesia). Coral Reefs, **17**: 23–28.

Elsdon, T.S., and Gillanders, B.M. 2002. Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fishes. Can. J. Fish. Aquat. Sci. **59**: 1796–1808.

Fennessy, S.T. 2000. Aspects of the biology of four species of Sciaenidae from the East Coast of South Africa. Estuar. Coast. Shelf Sci. **50**: 259–269.

Fransz, H.G. 1986. Effects of freshwater inflow on the distribution, composition and production of plankton in the Dutch coastal water of the North Sea. *In* The role of freshwater outflow in coastal marine ecosystems. *Edited by* S. Skreslet. NATO ASI (Adv. Sci. Inst.) Ser. Ser. G Ecol. Sci. **7**: 241–249.

Fritz, P. 1981. River waters. *In* Stable isotope hydrology: deuterium and oxygen-18 in the water cycle. *Edited by* J.R. Gat and R. Gonfiantini. International Atomic Energy Agency Tech. Rep. No. 210. pp. 177–201.

Gallo-Reynoso, J.P. 1998. La vaquita marina y su habitat critico en el alto Golfo de California. Gac. Ecol. (Instituto Nacional de Ecologia, SEMARNAP, Mexico, D.F.), **47**: 29–44.

Gao, Y.W., and Beamish, R.J. 1999. Isotopic composition of otoliths as a chemical tracer in population identification of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **56**: 2062–2068.

Galindo-Bect, M.S., Glenn, E.P., Page, H.M., Fitzsimmons, K., Galindo-Bect, L.A., Hernández-Ayon, J.M., Petty, R.L., Garcia-Hernandez, J., and Moore, D. 2000. Penaeid shrimp landings in the upper Gulf of California in relation to Colorado River freshwater discharge. Fish. Bull. **98**: 222–225.

Gleick, P.H. 2003. Global freshwater resources: soft-path solutions for the 21st century. Science (Washington, D.C.), **302**: 1524–1528.

Glenn, E.P., Lee, C., Felger, R., and Zengel, S. 1996. Effects of water management on the wetlands of the Colorado River delta, Mexico. Conserv. Biol. **10**: 1175–1186.

Glenn, E.P., Zamora-Arroyo, F., Nagler, P.L., Briggs, M., Shaw, W., and Flessa, K. 2001. Ecology and conservation biology of the Colorado River Delta, Mexico. J. Arid Environ. **49**: 5–15.

Goodwin, D.H., Schöne, B.R., and. Dettman, D.L. 2002. Resolution and fidelity of oxygen isotopes as paleotemperature proxies in bivalve mollusk shells: models and observations. Palaios, **18**: 110–125.

Grimes, C.B., and Kingsford, M.J. 1996. How do riverine plumes of different sizes influence fish larvae: do they enhance recruitment? Mar. Freshwater Res. **47**: 191–208.

Grossman, E.L., and Ku, T. 1986. Oxygen and carbon isotope fractionation in biogenic aragonite: temperature effects. Chem. Geol. **59**: 59–74.

© 2005 NRC Canada

Harding B.L., Sangoyomi, T.B., and Payton, E.A. 1995. Impacts of severe sustained drought on Colorado River water resources. Water Resour. Bull. **31**: 815–824.

Hernández-Aydn, J.M., Galindo-Bect, M.S., Flores-Báez, B.P., and Alvarez-Borrego, S. 1993. Nutrient concentrations are high in the turbid waters of the Colorado River Delta. Estuar. Coast. Shelf Sci. **37**: 593–602.

Høie, H., Otterlei, E., and Folkvord, A. 2004. Temperature-dependant fractionation of stable oxygen isotopes in otoliths of juvenile cod (*Gadus morhua* L.). J. Mar. Sci. **61**: 243–251.

Ingram, B.L., Conrad, M.E., and Ingle, J.E. 1996. Stable isotope and salinity systematics in estuarine waters and carbonates: San Francisco Bay. Geochim. Cosmochim. Acta, **60**: 455–467.

Jordan, D.S., and Gilbert, C.H. 1882. List of fishes collected by Luiet. Henry E. Nichols, U.S.N., in the Gulf of California and on the west coast of Lower California, with descriptions of four new species. Proc. U.S. Natl. Mus. **4**(227): 273–279.

Lankford, T.E., and Targett, T.E. 1994. Suitability of estuarine nursery zones for juvenile weakfish (*Cynoscion regalis*): effects of temperature and salinity on feeding, growth and survival. Mar. Biol. **119**: 611–620.

Lavín, M.F., and Sánchez, S. 1999. On how the Colorado River affected the hydrography of the upper Gulf of California. Continent. Shelf Res. **19**: 1545–1560.

Lavín, M.F., Godínez, V.M., and Alvarez, L.G. 1998. Inverse-estuarine features of the upper Gulf of California. Estuar. Coast. Shelf Sci. **47**: 769–795.

Longley, W.L. (*Editor*). 1994. Freshwater inflows to Texas bays and estuaries: ecological relationships and methods for determination of needs. Texas Water Development Board and Texas Parks and Wildlife Department, Austin, Texas.

Kalish, J.M. 1991*a*. Oxygen and carbon stable isotopes in the otoliths of wild and laboratory-reared Australian salmon (*Arripis trutta*). Mar. Biol. **110**: 37–47.

Kalish, J.M. 1991*b*. ^{13}C and ^{18}O isotopic disequilibria in fish otoliths: metabolic and kinetic effects. Mar. Ecol. Prog. Ser. **75**: 191–203.

Kowalewski, M., Avila Serrano, G.E., Flessa, K.W., and Goodfriend, G.A. 2000. Dead delta's former productivity: two trillion shells at the mouth of the Colorado River. Geology, **28**: 1059–1062.

Kucera, C.J., Faulk, C.K., and Holt, G.J. 2002. The effect to parental acclimation to spawning salinity on the survival of larval *Cynoscion nebulosus*. J. Fish Biol. **61**: 726–738.

Matlock, G.C. 1987. The role of hurricanes in determining year-class strength of red drum. Contrib. Mar. Sci. **30**: 39–47.

Meyer-Rochow, V.B., Cook, I., and Hendy, C.H. 1992. How to obtain clues from otoliths of an adult fish about the aquatic environment it has been in as a larva. Comp. Biochem. Physiol. A, **103**: 333–335.

Musick, J.A., Harbin, M.M., Berkeley, S.A., Burgess, G.H., Eklund, A.M., Findley, L., Gilmore, R.G., Golden, J.T., Ha, D.S., Huntsman, G.R., McGovern, J.C., Parker, S.J., Poss, S.G., Sala, E., Schmidt, T.W., Sedberry, G.R., Weeks, H., and Wright, S.G. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). Fisheries, **25**: 6–30.

Otterlei, E., Folkvord, A., and Nyhammer, G. 2002. Temperature-dependent otolith growth of larval and early juvenile Atlantic cod (*Gadus morhua*). J. Mar. Sci. **59**: 401–410.

Owen, O.S., and Chiras, D.D. 1995. Natural resource conservation management for a sustainable future. 6th ed. Prentice Hall, Englewood Cliffs, New Jersey.

Panella G. 1980. Growth patterns in fish sagittae. *In* Skeletal growth of aquatic organisms. *Edited by* D.C. Rhoads and R.A. Lutz. Plenum Press, New York. pp. 519–560.

Paperno, R., Targett, T.E., and Grecay, P.A. 2000. Spatial and temporal variation in recent growth, overall growth and mortality of juvenile weakfish (*Cynoscion regalis*) in Delaware Bay. Estuaries, **23**: 10–20.

Patterson, W.P. 1998. North American continental seasonality during the last millennium: high resolution analysis of sagittal otoliths. Palaeogeogr. Palaeoclimatol. Palaeoecol. **138**: 271–303.

Pitt, J., Luecke, D., Cohen, M., Glenn, E., and Valdes-Casillas, C. 2000. Two nations one river: managing ecosystem conservation in the Colorado River Delta. Nat. Res. J. **40**: 819–864.

Powell, G.L., Matsumoto, J., and Brock, D.A., 2002. Methods for determining minimum freshwater inflow needs of Texas bays and estuaries. Estuaries, **25**: 1262–1274.

Radtke, R.L., Shower, W., Moksness, E., and Lenz, P. 1998. Environmental information stored in otoliths: insights from stable isotopes. Mar. Biol. **132**: 347–348.

Rodriguez, C.A., Flessa, K.W., and. Dettman, D.L. 2001*a*. Effects of upstream diversion of Colorado River water on the estuarine bivalve mollusc *Mulinia coloradoensis*. Conserv. Biol. **15**: 249–258.

Rodríguez, C.A., Flessa, K.W., Téllez-Duarte, M.A., Dettman, D.L., and Avila-Serrano, G.A. 2001*b*. Macrofaunal and isotopic estimate of the former extent of the Colorado River estuary, upper Gulf of California, Mexico. J. Arid Environ. **49**: 185–195.

Román, M. 1998. Los sciaenidos en la reserva de la biosfera Alto Golfo de California. Pesca y Conservatión, **2**: 7–8.

Román, M., Barrera, G., and Campoy, J.F. 1998. La curvina golfina: ¿Volvió para quedarse? Voces del Mar, **1**: 1–2.

Secor, D.H., Dean, J.M., and Campana, S.E. 1995. Recent developments in fish otolith research. University of South Carolina Press, Columbia, S.C.

Stevenson, D.K., and Campana, S.E. 1992. Otolith microstructure examination and analysis. Can. Spec. Pub. Fish. Aquat. Sci. No. 117.

Thorrold, S.R., Campana, S.E., Jones, C.M., and Swart, P.K. 1997. Factors determining $\delta^{13}C$ and $\delta^{18}O$ fractionation in aragonitic otoliths of marine fish. Geochim. Cosmochim. Acta, **61**: 2990–2919.

Weidman, C.R., and Millner, R. 2000. High-resolution stable isotope records from North Atlantic cod. Fish. Res. **46**: 327–342.

Witbaard, R., Jenness, M.I., van Der Borg, K., and Ganssen, G. 1994. Verification of annual growth increments in *Arctica islandica* L. from the North Sea by means of oxygen and carbon isotopes. Neth. J. Sea Res. **33**: 91–101.

Wilber, D.H. 1992. Associations between freshwater inflows and oyster productivity in Apalachicola Bay, Florida. Estuar. Coast. Shelf Sci. **35**: 179–190.

Wurster, C.M., and Patterson, W.P. 2001. Late Holocene climate change for the eastern interior United States: evidence from high-resolution δ18O values of sagittal otoliths. Palaeogeogr. Palaeoclimatol. Palaeoecol. **170**: 81–100.

© 2005 NRC Canada

Evaluation of a US west coast groundfish habitat conservation regulation via analysis of spatial and temporal patterns of trawl fishing effort

Marlene A. Bellman, Scott A. Heppell, and Chris Goldfinger

Abstract: We examined the extent to which the 2000 Pacific Fishery Management Council footrope restriction shifted and reduced trawl fishing effort on Oregon fishing grounds, related these changes to the seafloor habitat type over which they occurred, and developed methods for enhancing spatial review of fishing effort. Density analysis of trawl start locations demonstrated how fishing efforts increased and decreased in relation to habitat distribution and fishery management actions between 1995 and 2002. Trawl effort patterns exhibited significant interannual variability and were patchy in distribution. Tow end-point locations from 1998 to 2001 were retrieved from manual logbooks for five reference sites located in proximity to rocky habitat. Trawl towlines were mapped and demonstrated a marked enhancement of fine-scale fishing effort resolution. Spatial shifts in fishing intensity (measured as kilometres towed) away from rock habitat were evident at all reference sites after the footrope restriction, with an average reduction of 86%. Some slight shifts into surrounding unconsolidated sediments also occurred. Our results indicate that the footrope restriction, in conjunction with associated landing limits, was effective in protecting rocky habitats from trawl fishing impacts. Continued spatial monitoring of trawl data would assist in fishery management assessment of conservation objectives for depleted groundfish and essential fish habitat protection.

Résumé : Nous examinons de quelle façon la restriction concernant les ralingues de fond imposée en 2000 par le Pacific Fishery Management Council a modifié et réduit l'effort de pêche au chalut sur les aires de pêche de l'Oregon; nous mettons ces changements en relation avec les types de fonds marins sur lesquels ils se sont produits; enfin, nous mettons au point des méthodes pour améliorer la surveillance spatiale de l'effort de pêche. Une analyse de densité des points de départ des chalutiers montre combien les efforts de pêche ont augmenté et diminué en fonction de la répartition des habitats et des activités d'aménagement de la pêche de 1995 à 2002. Les patrons d'effort de chalutage varient significativement d'une année à l'autre et suivent une répartition contagieuse. Nous avons obtenu les positions des points de départ et d'arrêt du chalutage des années 1998 à 2001 dans les livres de bord manuels pour cinq sites de référence situés près d'habitats rocheux. Nous avons transcrit sur des cartes géographiques les tracés de chalutage, ce qui se traduit par une amélioration marquée de la résolution de l'effort de pêche à petite échelle. Il y a des indications d'une réduction spatiale en moyenne d'environ 86 % de l'intensité de la pêche (évaluée en kilomètres de traits de chalutage) dans les habitats rocheux dans tous les sites de référence après la restriction des ralingues de fond. Il y a aussi des déplacements peu importants vers les sédiments meubles avoisinants. Nos données indiquent que la restriction des ralingues de fond, en conjonction avec les limites de débarquement associées, a protégé efficacement les habitats rocheux de l'impact de la pêche au chalut. La poursuite de la surveillance des données de chalutage pourrait être utile pour l'évaluation des objectifs de conservation en aménagement de la pêche pour la protection des populations décimées de poissons de fond et de l'habitat essentiel des poissons.

[Traduit par la Rédaction]

Introduction

There has been substantial concern over the effects of bottom trawling and other fishing activities on seafloor ecosystems and the sustainability of fish populations (Johnson 2002; National Research Council 2002; Dieter et al. 2003). Because bottom trawling alters essential fish habitat (EFH), it is important to understand fishing patterns both spatially and in the context of fishery management. Identifying both the distribution of seafloor habitat types and the spatial extent of

Received 22 November 2004. Accepted 5 May 2005. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 15 November 2005.
J18418

M.A. Bellman.[1] Cooperative Institute for Marine Resources Studies, Oregon State University, Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, OR 97365, USA.
S.A. Heppell. Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA.
C. Goldfinger. College of Oceanic and Atmospheric Sciences, Oregon State University, Marine Geology Active Tectonics Group, 104 Ocean Admin Building, Corvallis, OR 97331, USA.

[1]Corresponding author (e-mail: marlene.bellman@lifetime.oregonstate.edu).

 doi: 10.1139/F05-180 © 2005 NRC Canada

fishing effort over these habitat types is critical for evaluating where fishing gear impacts take place (Meaden 2000; Johnson 2002). The severity of fishing impact is determined by the intensity of fishing effort and the habitat where impacts occur (Jennings and Kaiser 1998; Auster and Langton 1999). Therefore, by shifting fishing effort between habitat types or reducing fishing intensity within habitat types, regulatory measures can act to protect the long-term sustainability of groundfish through conservation of EFH. It is imperative that the performance of fishery management measures implemented to protect depleted groundfish species and their associated habitat be critically evaluated. Previous studies reviewing the effects of Pacific groundfish management have rarely assessed spatial or habitat specific implications (Pikitch 1987; Gillis et al. 1995; Babcock and Pikitch 2000).

The Pacific Fishery Management Council has implemented a combination of management measures for the US west coast groundfish trawl fishery to protect and rebuild depleted rockfish (*Sebastes* spp.) populations (65 FR 221, 67 FR 57973). Many rockfish species are associated with hard-bottom, high-relief rocky areas (Love et al. 2002; McCain 2003). These areas are thought to have the greatest sensitivity to fishing impacts from mobile trawl gear because they are normally relatively stable and have high habitat complexity (substrate surface topography) with a prominent degree of biogenic cover (Auster and Langton 1999; Kaiser et al. 2002, 2003). When the structural and biogenic components of this habitat are reduced and damaged by trawling, obligate rockfish associations are diminished. The reduction of bottom trawling over rocky habitat is therefore an important component of any management strategy designed to avoid impacts to rockfish EFH.

The primary objective of this study was to examine trawl effort shifts over seafloor habitats in response to regulatory changes in the US west coast groundfish fishery. In particular, this study focused on a Pacific Fishery Management Council mandated restriction in trawl footrope size for landing nearshore and shelf rockfish species as well as most flatfish species. This regulation, enacted in 2000 to shift fishing incentives, linked various groundfish trip limits to large (>20.5 cm in diameter) and small (≤20.5 cm in diameter) footrope configurations (65 FR 221). By inhibiting the large footrope gear necessary to pass over rough terrain and obstructions, this restriction was designed to redirect fishing effort off of high-relief rocky areas where depleted rockfish species are most abundant. Furthermore, the retention of most fish normally caught in these areas was prohibited if using large footrope gear. A previous study by Hannah (2003), based solely on catch information, indicated that a reduction in fishing effort had occurred after the trawl footrope restriction but did not determine any relationship to seafloor habitat.

Comprehensive maps of seafloor lithology along the west coast of the United States have recently been compiled. Goldfinger et al. (2003) assembled and interpreted existing geological and geophysical data for the Oregon continental margin. The system used to describe surficial geologic habitat types was a modification of the classification described by Greene et al. (1999). Seafloor habitat, as defined for this study, refers to the surficial lithologic units dictating substrate type as described by Romsos (2004). While broader definitions of habitat may encompass many other ecological and abiotic factors, this study uses the seafloor substrate component as a proxy for associated fish communities (Hixon et al. 1991; Stein et al. 1992; Yoklavich et al. 2000).

Our analysis utilized methods for obtaining an adequate spatial resolution of fishing effort to review the relationship between targeted, patchy fishing effort and seafloor habitat features. The spatial resolution of fishing effort is determined by information reported by the fishery, yet to address different management issues, the proper resolution is required. Data collection procedures for the US Pacific west coast groundfish fishery include a tristate trawl logbook program (Sampson and Crone 1997). Trawl logbooks contain fishing location information, but prior to 1997, spatial resolution was poor because many locations were reported as the center point of large (10 × 10 nautical miles; 1 nautical mile = 1.852 km) reporting blocks. Trawl fishing effort is known to be concentrated in particular areas with patchy distribution (Larcombe et al. 2001; Marrs et al. 2002; Ragnarsson and Steingrimsson 2003), and seafloor habitats occur on a finer, more detailed scale than that of traditional reporting blocks. This contributes to potential bias when applying data values over coarse-scale blocks or grids (Rijnsdorp et al. 1998; Piet et al. 2000; Pitcher et al. 2000). Spatial resolution of fishing effort has also been limited in Oregon and Washington because electronic conversion of paper logbooks results in only the trawl start location being entered into electronic databases. A single point can limit our ability to review spatial patterns at the scale of actual fishing practices (e.g., tows can cover large distances, overlap, and cross arbitrarily defined grid cells).

This study was focused exclusively off the coast of Oregon and consisted of several components. First, an analysis of spatial and temporal shifts in trawl fishing effort over seafloor habitat was performed using available trawl start locations for the entire study period (1995–2002). This provided an initial spatial understanding of where increases and decreases in fishing effort occurred in relation to habitat distribution and fishery management measures. Second, tow end-point information from 1998 to 2001 was retrieved from manual logbooks for five reference sites located in proximity to rock habitat features. Trawl towlines were then mapped from start point to end point for finer scale resolution of fishing locations to enhance the examination of fishing effort shifts over seafloor habitat. Fishing intensity (measured as kilometres towed) was calculated to quantify fishing effort by habitat type. Finally, fine-scale spatial shifts in relation to the 2000 footrope restriction were then reviewed using trawl towlines.

Materials and methods

Commercial trawl logbook data were obtained for the limited entry groundfish fishery from state databases maintained by the Oregon Department of Fish and Wildlife (1995–2002), the Washington Department of Fish and Wildlife (1995–2001), and the California Department of Fish and Game (1995–2001). Washington and California data were filtered so that only trawls that occurred off the coast of Oregon were represented. Oregon data were not requested with

© 2005 NRC Canada

Table 1. Number and percentage of records filtered from raw logbook database records that were provided by each of the three states.

Filter applied	1995	1996	1997	1998	1999	2000	2001	2002	Total	% of total
Oregon										
Initial records	18 459	18 787	18 129	15 719	13 557	11 670	11 579	8 716	116 616	
Midwater gear	1 885	1 965	1 907	1 467	1 700	2 103	1 417	679	13 123	11.25
Center of block	1 520	1 678	665	27	19	0	0	0	3 909	3.35
Over landmass	39	53	74	33	85	53	2	4	343	0.29
Outside Oregon waters	5 500	4 939	4 520	4 694	4 011	3 215	3 235	3 096	33 200	28.47
Final records for analysis	9 515	10 152	10 963	9 498	7 742	6 299	6 935	4 941	32 845	
Washington										
Initial records	52	46	56	17	25	103	60	—	359	
Midwater gear	26	41	28	10	25	58	43	—	231	64.35
Center of block	16	7	0	0	0	0	0	—	23	6.41
Over landmass	0	0	0	0	0	0	0	—	0	0
Final records for analysis	10	5	28	7	0	45	17	—	112	
California										
Initial records	428	445	511	833	627	474	340	—	3 658	
Center of block	428	445	13	2	1	1	0	—	890	24.33
Over landmass	0	0	3	1	1	0	3	—	8	0.22
Final records for analysis	0	0	495	830	625	473	337	—	2 760	

Note: The resulting annual record totals were then used for analysis. Records were removed if the trawler used midwater gear, the set location was recorded as the center of a statistical reporting block, or the set location was accidentally noted over a landmass. California and Washington data were only requested for those logbook records that occurred in Oregon waters.

any geographical restriction and records extended into both Washington and California waters. These logbook records were removed from the analysis during the process of spatially joining annual fishing effort layers with a seafloor habitat layer exclusively off the Oregon coast. A single logbook record corresponds to an individual trawl tow and includes information pertaining to the vessel, date, time and location of tow, gear used, and catch. This study included only trawl tows using gear that contacts the seafloor. Unfortunately, it was impossible to review specific bottom trawl gear types used before and after the footrope restriction owing to the inconsistency of gear codes recorded by different states and the confounding use of a nonspecific groundfish trawl gear code before 2000. The application of data filters removed approximately 15% of Oregon logbook records, 25% of California logbook records, and 69% of Washington logbook records (Table 1).

Spatial analysis and mapping were conducted with ArcGIS desktop version 8.2 (Environmental Systems Research Institute, ESRI, Redlands, California). Data layers created and used in this study were all standardized using the same projected coordinate system (Universal Transverse Mercator Zone 10N) and datum (World Geodetic System of 1984) to minimize distortion of spatial properties in the study region and thus minimize spatial error in the analysis.

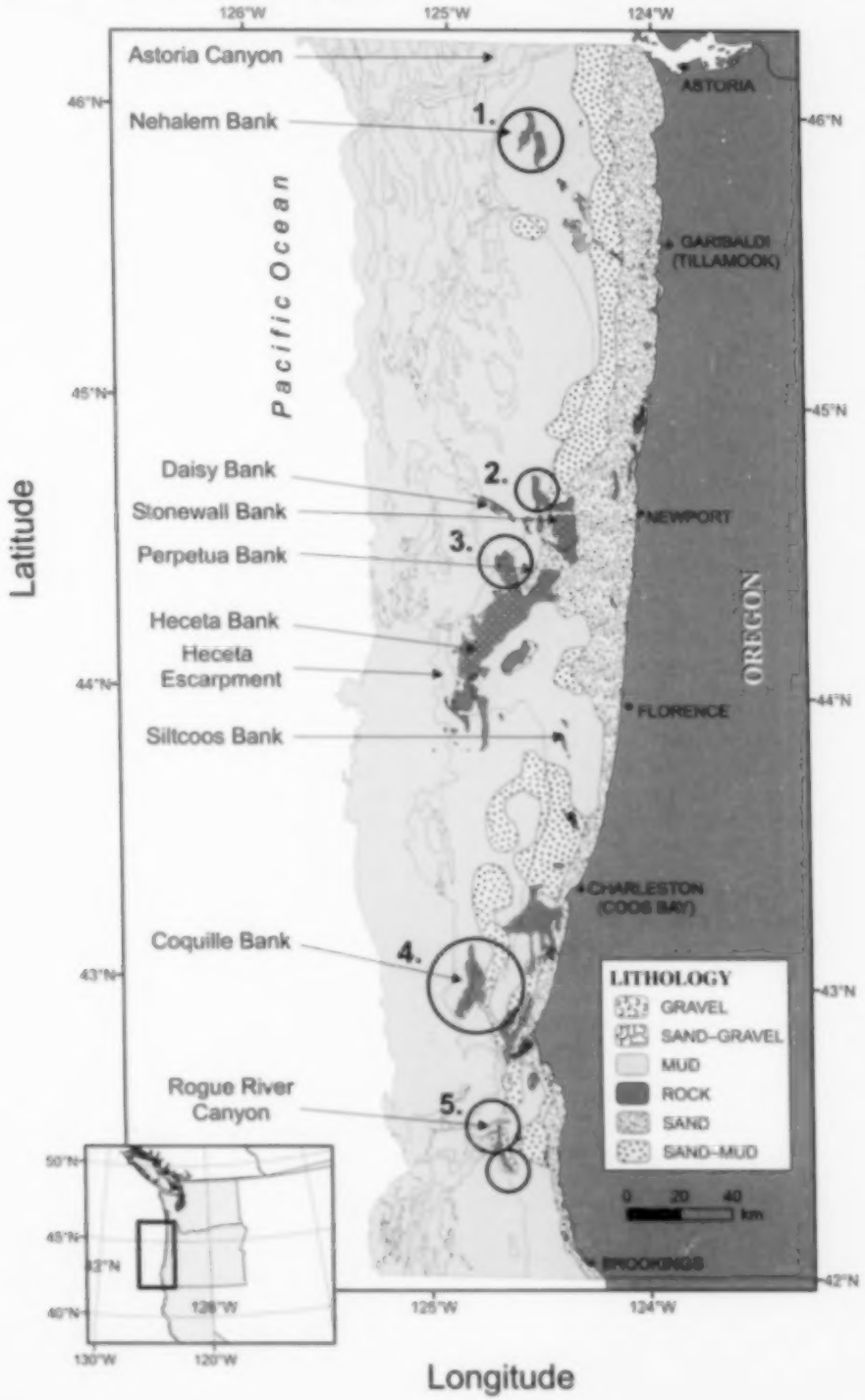
To begin reviewing trawl fishing effort, we mapped for each year and by state fishing fleet the locations where trawl fishing begins, referred to as the set of each tow. Fishermen are instructed to record the position where the brake is set, when all of the cable has been released for the appropriate depth in order for the net to be fishing on the seafloor. Trawl set locations from all three states' vessels were then combined into annual point (vector) layers of fishing effort in which each set location was represented by a single point. Oregon habitat polygons (rock, gravel, sand–gravel, sand, sand–mud, and mud) (Fig. 1), as described by Romsos (2004) and Goldfinger et al. (2003) were spatially joined to annual effort point layers to compute the geometric intersection between data layers to count the number of tows per year in each habitat type.

To observe the spatial shift in fishing effort between years, we converted each annual trawl set point layer to a continuous surface (raster) layer based on point density and then subtracted between years to observe areas of increased and decreased fishing effort. To identify patterns where trawl set points were concentrated, a density calculation measured the number of trawl set points contained within a given area and assigned this value to corresponding cells in a raster layer. We used a kernel density calculation per square kilometre with a 5-km search radius and an output cell size of 0.01 km^2. These parameters were selected to assure that the calculation and resulting patterns were a realistic representation of trawl fishing activities. Square kilometre area units have been previously used to represent trawl fishery-scale features (Kulka and Pitcher 2001). The search diameter used in this calculation was later verified to be within the average distance of trawl towline lengths (average = 11.86 km), which preserves the small-scale integrity of the data. Since each point is a representation of the set of a trawl tow, the calculation area should not extend beyond the area that could be covered during the average length of a trawl tow.

Five reference areas were selected by comparing spatial patterns of fishing effort with seafloor habitat type (Fig. 1). Four sites were selected that contained both rock habitat and significant fishing effort (sites 1–4). One additional site was selected, the Rogue River Canyon, with a greater proportion of soft sediment habitat and significant fishing effort (site 5). The ideal site area was determined and then used to select

© 2005 NRC Canada

Fig. 1. Location of reference sites (sites 1–5) in proximity to rock habitat and marine geomorphological features on the continental shelf off the west coast of Oregon, USA. Seafloor habitat data are represented in the lithologic units described by Goldfinger et al. (2003) and Romsos (2004). Reference site buffers (circles) indicate the area within which trawl start (set) locations were selected for further retrieval of trawl end (haul) locations in manual logbooks.



© 2005 NRC Canada

Table 2. Description of five selected reference sites and the logbook records from within these sites used to construct trawl towlines by retrieval of tow haul (end) locations.

	Site 1	Site 2	Site 3	Site 4	Site 5
Site description					
Site selection area diameter (km)	24	16	20	36	20 and 16
Mean reported site depth (fathoms)	102	94	101	160	166
Minimum reported site depth (fathoms)	51	53	60	39	50
Maximum reported site depth (fathoms)	250	185	320	650	600
Filtering process					
Initial selected Oregon logbook records	326	538	1442	1551	1350
Haul location missing	26	28	30	84	48
Haul location identical to set location	0	6	7	3	3
Haul location over landmass	0	0	1	5	1
Final records for analysis					
Oregon records	300	504	1404	1459	1298
Selected California records	—	—	—	71	429

Note: The filtering steps that were applied to identify and remove unsuitable records for this study are noted. 1 fathom = 1.8288 m.

trawl set points for further data retrieval. Two adjoining selection areas were used at the southern-most site (site 5) for optimal coverage of fishing effort patterns, which could not be adequately represented by a single selection. A subset of Oregon logbook records was created for each reference site (Table 2). Additionally, the data quality for habitat type (primarily rock) was assessed within each site area using ranked distributions of data density and quality, as developed by Romsos (2004). The order of rock habitat quality values ranked site 1 as the highest, followed closely by sites 2 and 4 with equal values, site 5 with a moderate value, and site 3 with the lowest value.

To improve the spatial resolution of fishing effort, we manually retrieved tow end locations, referred to as haul points, for each site's subset of records from paper logbooks held by the Oregon Department of Fisheries and Wildlife office in Newport, Oregon. A protocol was developed to assure data confidentiality and quality control. Logbook records that did not contain haul location information (4% of all reference site records) were removed from the analysis. Records with haul locations identical to the tow set location or for which trawling occurred over a landmass were also dropped from the analysis (<0.5%).

Trawl towlines were created using a Visual Basic script that drew a straight line from each set location to each corresponding haul location. The azimuth of each towline from true north (0°) was also calculated. The length of each towline was measured to estimate the distance that a vessel traveled. To determine if towline distances could have been traveled within a realistic range of towing speeds, we then used towline length to predict vessel speed based on the logbook-reported tow duration.

An overlay of trawl towlines across benthic habitat type subsequently split each towline into multiple segments at each habitat boundary and joined the attributes of the underlying habitat type to each towline segment. The length of each resulting towline–habitat type segment was measured and segment lengths were then summarized annually by habitat type. Patterns of trawl towlines were reviewed in both a spatial and a temporal context.

California logbook records were used for a comparison with the spatial and temporal patterns observed in towlines originating from Oregon logbook data. California state database logbook records from 1997 to the present contain the location for both tow set and tow haul. Subsets of California trawl towlines for the two southern reference sites (where Oregon and California fishing effort overlapped) were processed and mapped using the same methodology as for the Oregon reference site records noted above.

Swept area calculations, defined as the area of seafloor potentially contacted by trawl gear, were not made for the purposes of this study in part because of the absence of detailed trawl gear notation in logbooks and the variety of gear used in the fishery. Often, averaged gear parameters or those based on a fixed door spread are used in calculations for the purpose of swept area estimation (Ragnarsson and Steingrimsson 2003). The detailed spatial distribution of trawl towlines and towline distance measurements in this study provided similarly acceptable information to review fishing intensity. If detailed gear parameters and other influencing factors were adequately accounted for in the future, swept area estimates could be derived from our measurement of trawl towline distances.

A compilation of temporal management measures provided the basis by which corresponding fishing effort distributions were reviewed. Groundfish management measures for the limited entry trawl fishery were tabulated from the Federal Register for the time period 1995–2002. Acceptable biological catch, optimal yield, and annual allocation to the commercial trawl fishery were recorded by year for each managed species or fish assemblage (supplementary Table S1).[2] Cumulative trip limits were organized and recorded by month.

[2] Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 4035. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

© 2005 NRC Canada

Table 3. Results of the geographic overlay of tow set point locations and corresponding seafloor habitat type.

Lithologic unit habitat type	Total area of habitat (km^2)	1995	1996	1997	1998	1999	2000	2001	2002	Total
Tow set locations										
Sand–mud	4 236 922	1170	1398	1493	1520	1240	986	990	949	7 178
Sand	5 922 956	610	664	912	653	582	350	625	968	4 090
Mud	32 555 575	7081	7217	8343	7423	6219	5428	5560	2927	35 900
Rock	1 756 087	599	849	725	733	313	52	105	93	2 021
Gravel	7 489	0	0	0	0	0	0	0	0	0
Sand–gravel	37 606	65	24	13	6	13	2	0	0	34
Porportion of tow set locations										
Sand–mud		0.123	0.138	0.130	0.147	0.148	0.145	0.136	0.192	0.146
Sand		0.064	0.065	0.079	0.063	0.070	0.051	0.086	0.196	0.083
Mud		0.743	0.711	0.726	0.718	0.743	0.796	0.764	0.593	0.729
Rock		0.063	0.084	0.063	0.071	0.037	0.008	0.014	0.019	0.041
Gravel		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sand–gravel		0.007	0.002	0.001	0.001	0.002	0.000	0.000	0.000	0.001

Note: Results are noted as both the number and the proportion of tow set locations over each habitat type. The total mapped area of each habitat type is also noted.

In-season changes to trip limits were added to these tables for each management change that took effect during the course of a year (supplementary Table S2).[2]

Results

A decreasing trend in annual trawl fishing effort off the Oregon coast was observed across all years from 1997 to 2002 (Table 1). Directed fishing effort in Oregon waters by Washington vessels was concentrated along the Oregon–Washington border and diffused in a southerly direction. California trawl effort was concentrated at the Oregon–California border and diffused gradually in a northerly direction.

Trawl fishing effort differed by location and intensity in proximity to major rocky bank features on the Oregon continental shelf (Fig. 1). Trawl set points over Nehalem Bank occurred predominantly over western portions of the bank. On Stonewall Bank, there was a concentration of set points along the north to northwest slope edge of the bank but very few over the main bank. Perpetua Bank had a similar concentration of set points around the northwest slope edge portion of the bank but again, very few points over the main bank. Trawl set points were located throughout the Heceta Escarpment, the slope edge just offshore of Heceta Bank, with only a few points appearing over the southern tip of the actual bank itself. Siltcoos Bank did not have any associated trawling activity. Coquille Bank displayed set point patterns to the north, south, and west of the bank, with a lesser density of set points directly over the main bank.

In addition to an overall decline in effort, there were shifts in the number of trawl sets between years and between habitat types (Table 3). Trawl set points for the entire study period were within mapped seafloor lithology, which extended to approximately the 3000-m depth contour. The number of trawl sets per habitat type was positively correlated with the total area of habitat type available (i.e., the majority of trawl sets took place in the largest geographically mapped habitat type: mud). The smallest extent of mapped habitat, gravel habitat, did not contain any trawl set locations, although it is still possible that actual trawl tows may cross into this habitat designation.

Broad-scale spatial shifts in trawl fishing effort distribution were apparent between years, as visualized by density maps (Fig. 2). The location of areas experiencing increases and decreases in fishing effort are summarized in Table 4. Areas of increased fishing effort were still evident in each between-year calculation, despite the overall decline in trawl tows each year. This provided clear evidence that trends or shifts in effort are occurring that were not attributed solely to the decrease in annual tow numbers. The continuous decrease in fishing effort along the outer continental shelf in 2002 relative to fishing effort in 2001 is attributed to the first depth-related spatial closure of the fishery from approximately 100 to 250 fathoms (1 fathom = 1.8288 m) in September of 2002 (67 FR 57973). A large portion of the continental shelf was closed to trawling through establishment of the Darkblotched Rockfish Conservation Area to protect overfished darkblotched rockfish (*Sebastes crameri*). Even though this closure was only reflected in the study data for 4 months at the end of the fishing year, it nevertheless was revealed as a marked decrease in fishing effort throughout the closure boundaries.

The use of trawl towlines created for each reference site demonstrates a substantial improvement in the resolution of fishing effort data relative to the use of start-point locations alone. Towlines provide an enhanced visual representation of spatial fishing patterns to detect changes or shifts in trawl towing behavior relative to habitat, bathymetry, and tow direction. Based on an azimuth calculation from true north (0°) for each towline, the majority of towlines are positioned within northern (315–45°) or southern (135–225°) directional quadrants (Table 5). The straight-line towline model is a conservative estimate of actual distances trawled owing to the many factors that prevent towing in exactly straight lines. Predicted vessel speeds derived from towline length and logbook duration fell within a realistic range of towing speeds (1.8–3.0 knots) established from interviews conducted with

© 2005 NRC Canada

Fig. 2. Density maps of the extent and degree of increase or decrease in trawl fishing efforts calculated by subtracting an annual set location density layer from the density layer of the previous year (calculated for each year pair between 1997 and 2002). Fishing effort change is represented by a spectrum from areas of decrease (blue) to no change (yellow), to areas of increase (red).

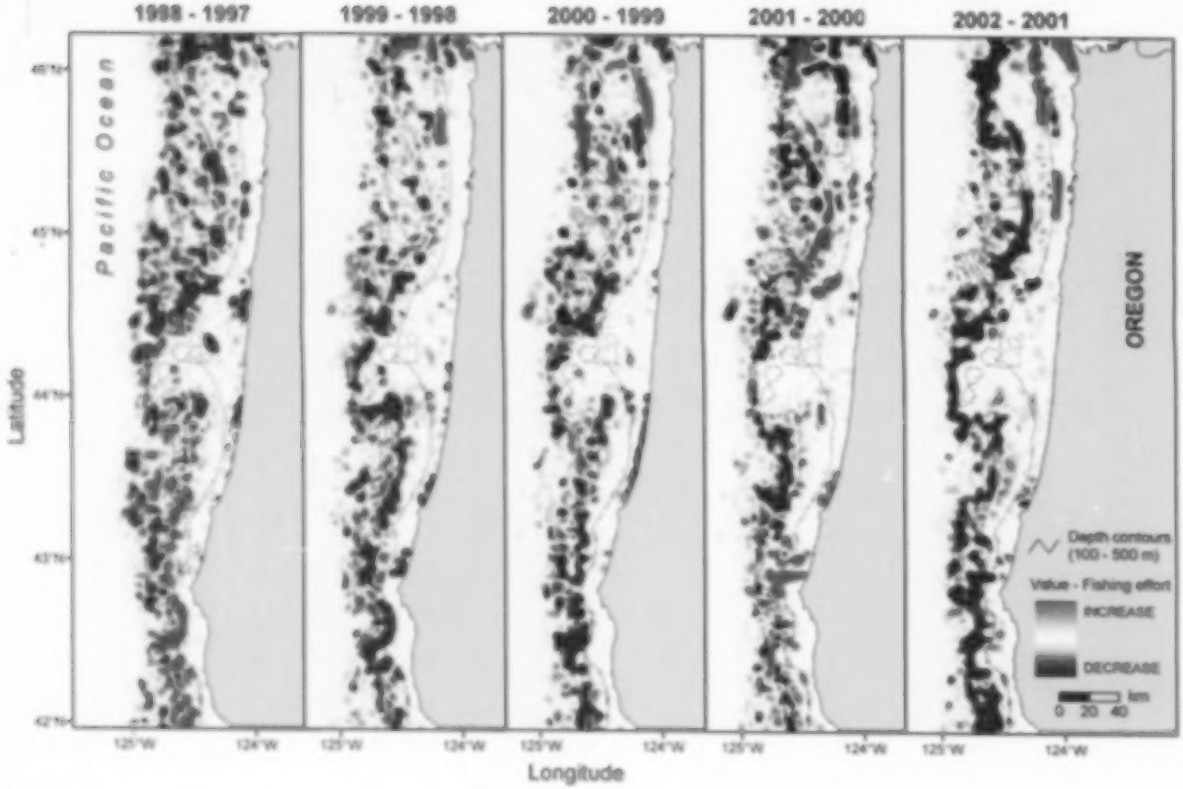


Table 4. Summary of major locations off the Oregon coast experiencing increasing and decreasing trawl fishing effort calculated by subtracting an annual set location density layer from the density layer of the previous year.

Annual difference	Increased effort	Decreased effort
1998–1997	Largely located from central to southern Oregon on the continental margin between the 100- and 200-m contours, with patchy distribution along the entire margin	Patchy decreases observed from nearshore to deep offshore regions but concentrated mostly along the northern border west of Astoria and extending into central Oregon along the 200-m contour
1999–1998	Concentrated along the northern border west of Astoria with additional light increases in deeper water offshore along the entire margin	Concentrated in a semisolid band from Depoe Bay to the southern Oregon border along and just inshore of the 200-m contour
2000–1999	Primarily located in the northern region both along the 100-m contour and in deeper offshore waters past 300 m	Several concentrated areas are west of Astoria and Newport and also in the southern region from Bandon to Brookings between the 100- and 300-m contours
2001–2000	From the northern border to central Oregon between the 200- and 300-m contours with several patches centrally located along the 100-m contour; additional patches are located between Bandon and Port Orford	Noted in the northern region along the 100-m contour and also offshore in deeper waters both north and south of Heceta Bank
2002–2001	Only several small patches are noted in the northern region, two west of Astoria (at <50 and 100 m) and one between Netarts and Pacific City from the 50- to the 100-m contour	Observed in a large band along the entire continental margin focused at the 200- to 300-m contours

Note: Effort shifts were calculated for each year pair between 1997 and 2002, with effort in the previous year subtracted from effort in the most recent year in the pair.

© 2005 NRC Canada

Table 5. Percentage of reference site trawl towlines that lie within each directional quadrant based on their azimuth (calculated from true north (0°)).

	Site 1	Site 2	Site 3	Site 4	Site 5
North–south quadrants (315°–45° and 135°–225°)	90	77	84	89	65
East–west quadrants (45°–135° and 225°–315°)	10	23	16	11	35

fishermen. This evidence supports the assertion that the trawl towline model is a close approximation of reality, although the model cannot determine the exact path that a vessel trawled.

Spatial shifts in fishing effort away from rock habitat were strikingly evident for all reference sites after the 2000 footrope restriction (Fig. 3). Fishing intensity was calculated as the kilometres towed per year for a given habitat type. Total distance trawled over each habitat type was pooled for the 2 years prior to the footrope restriction (1998–1999) and the 2 years after its implementation (2000–2001) (Table 6). There is a distinct difference between just counting the number of total trawl tows over each habitat type (number of towline segments) and getting an estimate of actual fishing distances covered over each habitat. Decreasing fishing intensity and a decreasing number of towlines segments over rock habitat are demonstrated for all five reference sites after the footrope restriction. Fishing intensity decreases were greatest after the footrope restriction at site 2 (93.7% reduction) and site 1 (93.6% reduction). Site 5 demonstrated a 90% reduction followed by reductions of 84.8% at site 3 and 69% at site 4. Increasing fishing intensity is shown over mud habitat at sites 1 and 4, although the number of towline segments decreases slightly. Smaller increases occur over sand habitat at sites 1, 3, and 4. Site 3 demonstrates a small increase in towing distance over sand habitat, despite a decrease in the number of towline segments represented.

In general, spatial towline patterns of Oregon and California vessels at site 5 are consistent, but Oregon towlines demonstrate two additional fishing patterns. Oregon vessels also trawl within and along the length of the canyon and over an area just south of the canyon at depths of approximately 150–200 m. These trawl patterns are closely associated with the bathymetric features of the Rogue River canyon. The canyon's east–west orientation reflects the higher percentage of towlines positioned within east and west directional quadrants at site 5 (Table 5). The majority of California tows began north of the canyon and trawling occurred in a northerly direction. A second group of tows by California vessels began in the southwestern section of the upper site 5 selection area and towed south along the 400-m contour. The third group of tows by California vessels began in the southwestern section of the lower site 5 selection area at depths greater than 150 m and trawled in a southeasterly direction. California vessel towlines in site 4 were consistent with Oregon towline spatial patterns. Most of the California set points were located in the southern half of the site 4 selection area and trawling occurred in a southerly direction.

Discussion

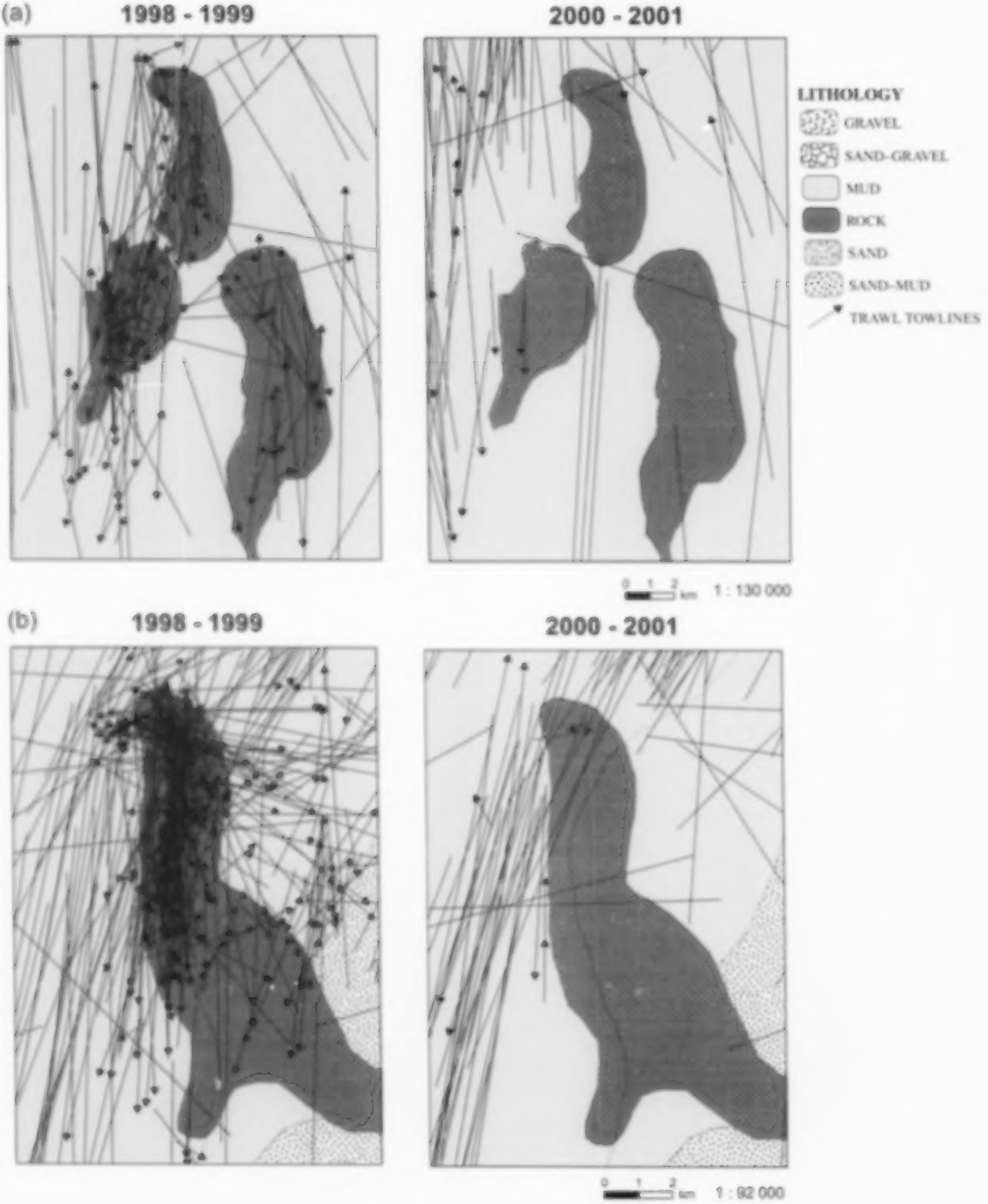
There is significant interannual variability in bottom trawl fishing effort off the Oregon coast. These interannual shifts are affected by factors such as changes in target species, trip limit regulations, and fishing strategies (Babcock and Pikitch 2000; Sampson 2001). Overall, Oregon bottom trawl fishing effort exhibited patchy distribution and maintained similar statewide patterns over the entire study period. This consistency is common when fishermen return to areas previously known to harbor high abundances of target species and suitable seafloor for trawling.

The evaluation and continuous monitoring of spatial fishing effort distributions within various habitats will be a critical component in executing management decisions for habitat conservation objectives. Patchy distribution of trawl effort typically disturbs the same areas of seabed frequently but in turn leaves large areas unaffected by the impacts of mobile fishing gear. From a conservation standpoint, patchy fishing distribution may be acceptable because those areas have already been altered by repeated disturbance, as long as fishing efforts do not expand into previously unaffected areas of high-quality habitat. However, conservation objectives may also choose to review which habitats or nontarget species are located within already targeted fishing grounds to reduce impacts on those habitat types or species particularly sensitive to fishing pressure. Spatial management measures, such as closed areas, can have the potentially undesirable effect of shifting fishing activity to areas that were previously lightly fished or very rarely fished (Rijnsdorp et al. 2001; Holland 2003). Therefore, the mitigation of a closed area should be carefully weighed against the potential for redistribution of fishing effort. Larcombe et al. (2001) demonstrated that a redistribution of trawl fishing effort unrelated to closed areas tended to concentrate in relatively small, high-effort areas rather than expanding into new fishing grounds. Using finer-scale spatial analysis, such as the trawl towline model, it is possible to identify whether fishing effort is localized to a small area or the same amount of fishing effort is spread out over a larger area. These two different spatial patterns of fishing effort have not been clearly addressed by fishing impact and recovery studies.

Density mapping creates views of aggregated fishing effort that closely reflect habitat-related patterns usually undetected by grid methods, unless the grids are perhaps set at very fine scales (i.e., ≤1 km × 1 km cells). A grid method splits geographical space into a pattern of arbitrarily sized cells and assigns fishing effort homogeneously within each cell. Grid cell size has a large influence on the results of such work. Grid cell size can either be too small and fishing practices overlap into multiple cells or too large and assigned fishing effort is too broadly distributed. Another concern is that grid cells are often unable to reflect the spatial complexity of geographic features, such as habitat boundaries, an issue addressed by this work. Density mapping greatly facilitated the identification and extent of particular habitat areas that were experiencing changes in fishing pressure, which aided in the selection of study sites. Another brief consideration is that density mapping provides an eas-

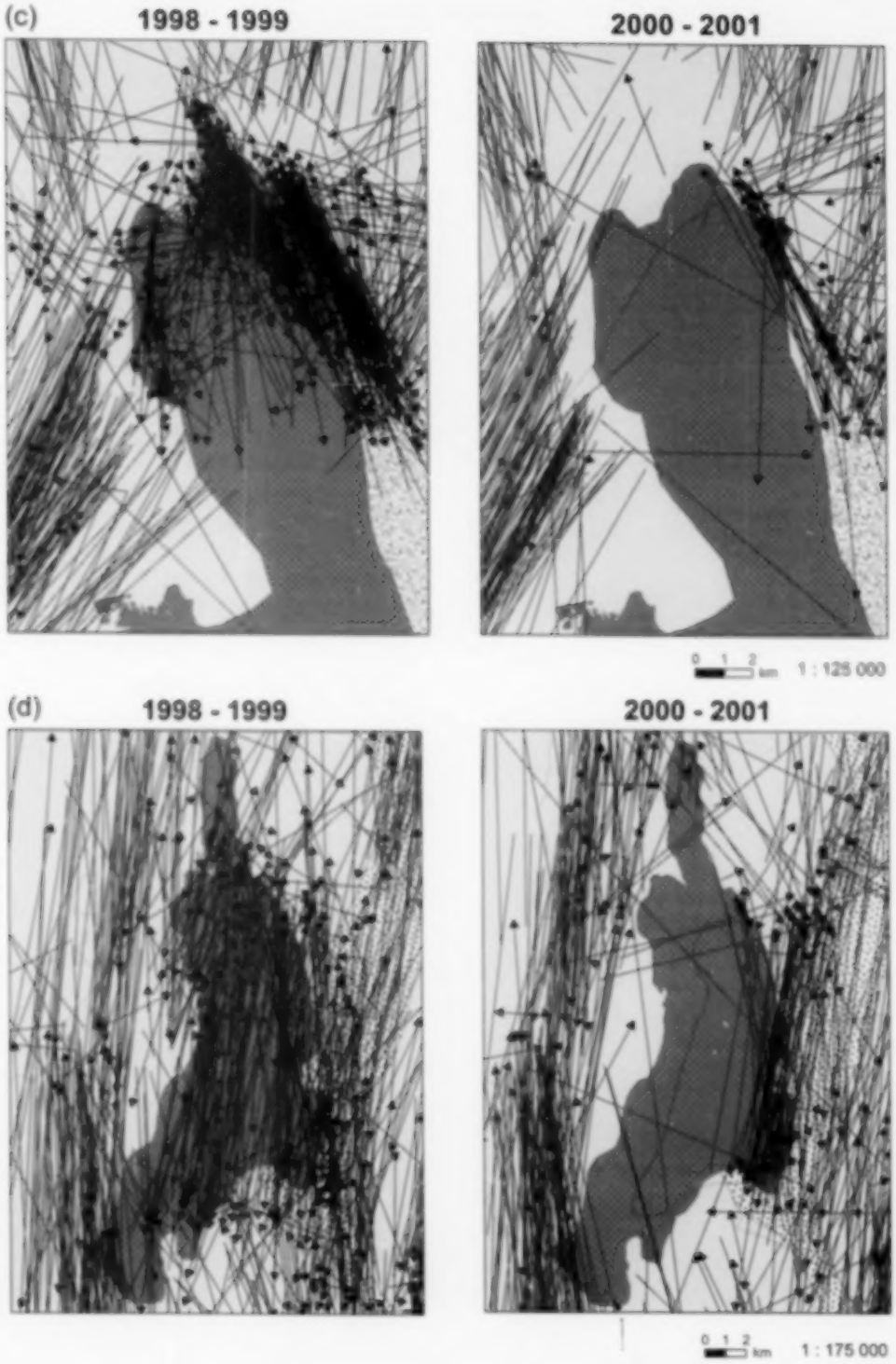
© 2005 NRC Canada

Fig. 3. Spatial shifts in trawl effort away from rock habitat at five selected reference sites before (1998–1999) and after (2000–2001) the footrope restriction. See Fig. 1 for reference site locations. Note the scale changes between sites. (*a*) site 1; (*b*) site 2; (*c*) site 3, (*d*) site 4; (*e*) site 5.



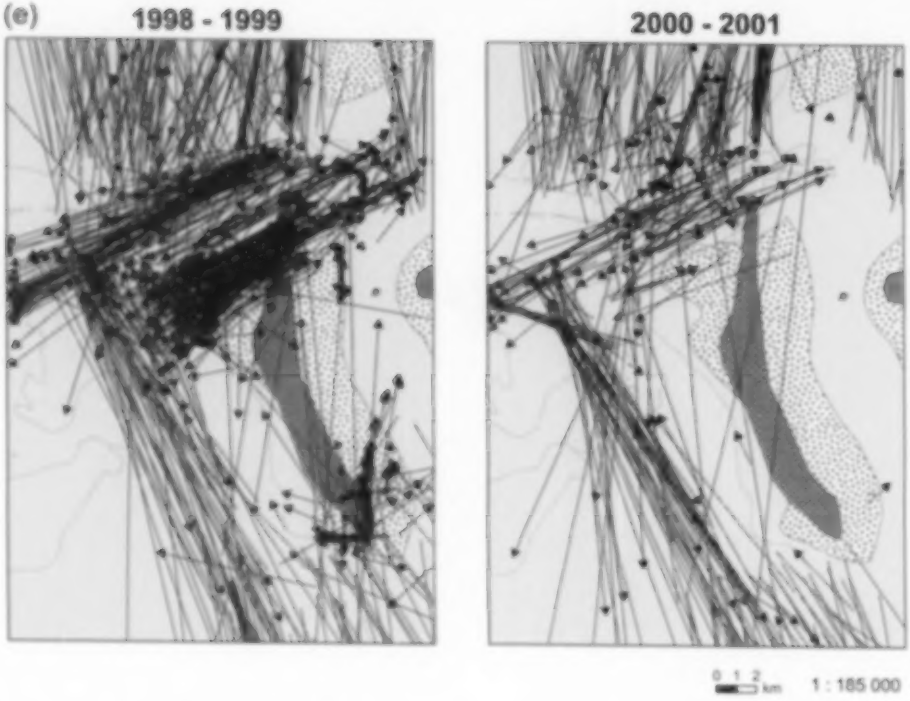
© 2005 NRC Canada

Fig. 3 (*continued*).



© 2005 NRC Canada

Fig. 3 *(concluded).*



ily aggregated view of trawl start locations, which is often necessary when working with any confidential fishery-dependent data. Confidentiality concerns can still be addressed by this method and yet the spatial resolution of fishing effort patterns is improved.

The use of complete trawl towlines rather than only set points resulted in the analysis of fleet responses to management measures at a scale appropriate to evaluate the linkages between fishing effort and particular seafloor habitats. Trawl towlines can more accurately represent the distribution of fishing effort and intensity in geographic space as well as provide a basis by which to observe patterns of fine-scale yet realistic fishing effort. Based on this analysis, it is crucial that in the future all haul location data be entered into electronic databases maintained by fishery-dependent collection programs. Because haul locations have been and are currently provided by fishermen in paper logbooks, it would require only a minimal cost to include this field in the data entry process. The annual review and processing of spatial data would not only provide an additional quality control step by verifying realistic reporting of fishing location but also allow evaluation of current spatial management measures. Although this study focused on five reference sites off the Oregon coast, this work could easily be expanded to examine all trawl logbook data for the US west coast.

The spatial shift of tow patterns away from rock habitat was distinctly evident from visualization of trawl towlines after the 2000 Pacific Fishery Management Council footrope restriction. Towline analysis also provided a measurement of trawling intensity by habitat type. The reduction in towing over rocky habitat at our reference sites was both visibly evident and clearly measured by intensity with an average ~86% change. The reduction in effort over rocky habitat did not simply result in overall reduced fishing effort, as some fishing effort shifted from rock habitat to surrounding areas of unconsolidated sediments. The outcome of management measures should be considered and reviewed as to the extent of such trade-offs between fishing impact on hard- versus soft-bottom habitats and possible effects on other groundfish species EFH.

We observed a majority of north–south tow directions, with the exception of east–west towing related to the Rogue River canyon bathymetry in southern Oregon. This supports previous observations by Friedlander et al. (1999) that trawl marks on the California seafloor are commonly oriented parallel to bathymetric contours and by Marrs et al. (2002) that trawl vessels followed depth contours parallel to the shoreline. Models of US west coast trawl fishing effort based on set locations could be fine-tuned by incorporating spatial parameters related to depth contour tow direction (National Marine Fisheries Commission 2005; Scholz et al. 2005).

Trawl gear disturbance on the seafloor can be examined through the use of high-resolution side-scan sonar (Krost et al. 1990; Friedlander et al. 1999), but the towline model can more efficiently quantify fishing effort. The path covered by a trawl, or trawl track, is often visible on sonographs as a long, narrow, linear depression. Side-scan sonar is costly and the detectability of trawl tracks is heavily dependent on timing of the side-scan survey and the time at which fishing occurred, while trawl towlines display fishing activity at the scale of the fishery and provide an enduring (if indirect) record of potential trawl tracks. Furthermore, side-scan sonar

© 2005 NRC Canada

Table 6. Total trawl towline distances and the number of towline segments over seafloor habitat type before (1998–1999) and after (2000–2001) the footrope restriction.

	Rock			Mud			Sand			Sand–mud		
Reference site	1998–1999	2000–2001	% change	1998–1999	2000–2001	% change	1998–1999	2000–2001	% change	1998–1999	2000–2001	% change
Towline distances (km)												
Site 1	403	25	–93.6	1340	2071	54.6	0	10	>100.0	39	51	29.7
Site 2	764	49	–93.7	1977	1402	–29.1	70	7	–89.4	518	300	–42.0
Site 3	1670	253	–84.8	6487	5731	–11.6	116	124	6.9	17	2	–88.4
Site 4	2049	636	–69.0	6924	7243	4.6	7	15	94.3	1929	1807	–6.3
Site 5	232	22	–90.4	7763	4913	–36.7	40	18	–54.5	1057	150	–85.8
Towline segments (no.)												
Site 1	450	37	–91.8	224	205	–8.5	0	1	100.0	8	9	12.5
Site 2	166	16	–90.4	402	133	–66.9	12	3	–75.0	90	54	–40.0
Site 3	906	135	–85.1	1329	760	–42.8	102	62	–39.2	2	1	–50.0
Site 4	579	257	–55.6	1436	1340	–6.7	2	5	>100.0	469	483	3.0
Site 5	203	12	–94.1	2638	1163	–55.9	18	6	–66.7	553	41	–92.6

Note: A towline segment represents one sections of a towline after it was split at each habitat polygon boundary (i.e., multiple towline segments can be created by splitting an individual towline).

may not detect trawl tracks in hard-bottom habitats. However, these two methods may prove to be complementary. Reviewing trawl towlines may provide the first step for identifying areas where high fishing impact disturbance occurs and trawl marks could then be examined closely with the use of side-scan sonar to verify effort patterns from logbook data and which habitats have been impacted.

Our results indicate that the footrope restriction, in conjunction with associated landing limits, was effective in protecting rocky habitats from trawl fishing impacts. This supports previous demonstrations that gear changes or modifications can achieve some purposeful level of habitat conservation (Van Marlen 2000; Valdemarsen and Suuronen 2003). Fishery managers often only manage for direct habitat conservation if forced by legislation or if it is demonstrated that a loss of habitat would directly lead to a loss of yield in the fishery. Similarly, in this case, although the footrope regulation was only indirectly aimed at habitat conservation, it ultimately served this purpose.

Future extensions of this research will need to incorporate analysis of catch data to clarify the effects of gear restriction versus trip limits. One possible method described by Larcombe et al. (2001) apportions catch equally along the length of a towline and then summarizes catch within a fine-scale grid of 1-km^2 cells. Branch et al. (2005) utilizes a clustering method related to trawl towline locations and associated catch data, which could then be used to delineate groups of tows in specific areas and their associated target species. This method would be useful for understanding various patterns of targeting fishing at or near the rocky banks examined in this study.

This study directly evaluated the effects of a specific preceding management action, which is not often done in the context of fishery management today. Substantial regulatory changes have occurred in the last decade that have ultimately resulted in a reduction in trawl fishing effort off the Oregon coast. Tracking of regulatory change by species provides the foundation to spatially examine individual management measures in a multispecies groundfish fishery. Effort shifts can be studied on any time step, from arbitrary (i.e., 1 year) to more natural steps, like regulatory regime shifts. Fishery management compilation tables created for this study have been valuable tools in both research and outreach but to our knowledge do not exist outside of our work. It is recommended that this type of systematic tracking be instituted formally as a required exercise for management purposes and that these materials be made readily available to all stakeholders.

It will be necessary to continue monitoring spatial responses in fishing effort to evaluate sustained habitat protection. Based on this monitoring information, an adaptive management process could learn from and adapt to changing circumstances in the fishery to influence habitat conservation (Cicin-Sain and Knecht 1998). Through the existing management process, trip limits and gear restrictions associated with the original 2000 footrope regulation have since been adjusted. Depth-based spatial management closures were implemented in September 2002 and related closures continued into 2003. Rock habitats within reference sites were not protected by these depth-based closures until May 2003. Therefore, the observed patterns in fishing effort reviewed

© 2005 NRC Canada

here were based solely on previous management strategies. Potential rock habitat recovery from trawl impacts at our study sites began prior to the full spatial closure.

Reference site areas have been identified where EFH recovery is likely occurring off the coast of Oregon. These reference sites should be studied in situ as soon as possible to begin answering fundamental questions regarding recovery rates of habitat in the absence of trawling. A limited number of studies have been published that were designed to determine the recovery of rocky habitats upon removal of fishing impacts (Freese et al. 1999; Freese 2001). Research gaps still exist in the determination of event–response relationships as a function of gear, recovery time, and habitat type, especially in naturally stable, structurally complex habitats such as rocky reef habitat (Collie et al. 2000; Kaiser et al. 2002). For benthic communities that have experienced chronic fishing disturbance, it is not known whether eventual recovery to a former (often unknown) state will occur if fishing is halted or if the system might have reached an alternative stable state from which it cannot simply return following removal of fishing disturbances (Holling 1973; Holling et al. 1995). It is generally thought that at high fishing effort levels, initial reductions would decrease impacts marginally but that benefits would be more apparent as effort declined even further (National Research Council 2002). The reference sites identified in this study can be used for future research to provide additional insight in understanding such concepts.

By integrating new information on seafloor substrate at finer scales or by including ecological habitat factors, examining the effects of fishing effort distribution and intensity in the context of EFH would be enhanced. Habitat as defined in this study is fairly limited in the framework of groundfish EFH. Numerous studies have shown correlations between demersal fish and various classifications of seafloor substrate (Matthews 1989; McRea et al. 1999; Nasby-Lucas et al. 2002). New information on aspects of fish–habitat associations such as depth, temperature, salinity, biogenic structure, and nutrient or prey availability could be incorporated into the research methods of this study.

Results also demonstrate the necessity of improving the spatial resolution of fishery data to address current fishery management concerns. Limitations on spatial precision are ultimately tied to the accuracy of the original positions recorded in logbooks. The precision of fishing location using the global position system (GPS) is an improvement over Loran A and C, which were the shore-based navigation systems used prior to the implementation of GPS. Spatial precision works to the fishermen's advantage because they can place their gear more accurately with the aid of GPS chart plotters and supplementary acoustic equipment. Since the mid-1990s, the spatial precision of logbook data has also benefited from required recording of actual tow location in trawl logbooks and from observers' independent monitoring of fishing activities. Implementation of electronic vessel logbook systems to monitor fisheries would be effective in providing accurate and timely spatial data to improve fisheries management (Meaden 2000; National Research Council 2000). These systems would shorten the lag time that presently exists in the availability of data and facilitate utilization of spatial data on fishing catch and effort as a means to directly evaluate management of the fishery. Vessel monitoring systems may assist in verifying spatial location and patterns of fishing from individual tows, but this would require linkage to detailed fishing logbooks that host all of the other data fields associated with an individual tow during a particular fishing trip (Rijnsdorp et al. 1998; Kemp and Meaden 2002; Marrs et al. 2002). At this point in time, vessel monitoring systems in the US west coast groundfish fishery may not be useful for management purposes other than basic enforcement of spatial area violations. If the frequency of vessel location transmissions were increased or detailed trawl track data from position loggers were available, other fishing patterns, such as lifting trawl doors and resetting the same tow in a different direction, could be addressed. Until then, trawl towlines are one method by which we can improve fishing effort resolution.

Although extensive information is contained in logbooks, these data have been underutilized in fisheries management (Starr and Fox 1996; National Research Council 2000). This study's use of fishery-dependent logbook data demonstrates the extensive geographic and temporal coverage that these data contain relative to fishery-independent data sources. Research survey tows originating from reference sites were less than 1% of the fishing intensity by commercial tows selected from the same sites. Observer coverage and increases in collaborative research are incorporating more fishery-dependent data sources into the management arena (National Research Council 2004). Examining previous years' fishing effort data before considering future regulation changes may work to alleviate concerns by fishermen that fishery managers do not value the information that they provide (Kaplan 1998; Gilden and Conway 2002). With the recent shift to a 2-year groundfish management cycle (68 FR 52519) and improvements in earlier availability of fishery-dependent data, this can now be a realistic expectation when considering future policies and regulations.

In summary, this study demonstrated that the 2000 Pacific Fishery Management Council footrope restriction and associated landing limits shifted trawl fishing effort away from the rocky habitat of depleted rockfish (*Sebastes* spp.) off the Oregon coast. Methodologies developed in this study highlight the benefits of increasing the spatial resolution of fishery data collection. New information on relationships between groundfish and habitat type, advances in seafloor mapping and habitat classification, and ongoing changes in fishery management will each contribute valuable information to future analyses of this type. Careful review and monitoring of spatial data from the US west coast groundfish trawl fishery can assist in evaluating the extent and type of habitat affected by fishing disturbances and which management measures influence habitat conservation.

Acknowledgements

This research was supported by an award to the Cooperative Institute for Marine Resources Studies from the Northwest Fisheries Science Center of the National Marine Fisheries Service to S.A.H. The statements, findings, conclusions, and recommendations are those of the authors and do not necessarily reflect the views of the National Marine Fisheries Service. We acknowledge the valuable feedback provided by Oregon fishermen, with assistance from the Port Liaison Project. Special

© 2005 NRC Canada

thanks go to Chris Romsos, Waldo Wakefield, Mark Saelens, and Mark Freeman for their support. We also thank Curt Gault for his assistance with data entry.

References

Auster, P.J., and Langton, R.W. 1999. The effects of fishing on fish habitat. *In* Fish habitat: essential fish habitat and rehabilitation. *Edited by* L.E. Benaka. Am. Fish. Soc. Symp. 22. American Fisheries Society, Bethesda, Md. pp. 150–187.

Babcock, E.A., and Pikitch, E.K. 2000. A dynamic programming model of fishing strategy choice in a multispecies trawl fishery with trip limits. Can. J. Fish. Aquat. Sci. **57**: 357–370.

Branch, T.A., Hilborn, R., and Bogazzi, E. 2005. Escaping the tyranny of the grid: a more realistic way of defining fishing opportunities. Can. J. Fish. Aquat. Sci. **62**: 631–642.

Cicin-Sain, B., and Knecht, R.W. 1998. Integrated coastal and ocean management: concepts and practices. Island Press, Washington, D.C.

Collie, J.S., Hall, S.J., Kaiser, M.J., and Poiner, I.R. 2000. A quantitative analysis of fishing impacts of bottom fishing on shelf-sea benthos. J. Anim. Ecol. **69**: 785–798.

Dieter, B.E., Wion, D.A., and McConnaughey, R.A. (*Editors*). 2003. Mobile fishing gear effects on benthic habitats: a bibliography. 2nd ed. NOAA Tech. Memo. NMFS-AFSC-135.

Freese, L. 2001. Trawl-induced damage to sponges observed from a research submersible. Mar. Fish. Rev. **63**(3): 7–13.

Freese, L., Auster, P.J., Heifetz, J., and Wing, B.L. 1999. Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Mar. Ecol. Prog. Ser. **182**: 119–126.

Friedlander, A.M., Boehlert, G.W., Field, M.E., Mason, J.E., Gardner, J.V., and Dartnell, P. 1999. Sidescan-sonar mapping of benthic trawl marks on the shelf and slope off Eureka, California. Fish. Bull. **97**: 786–801.

Gilden, J., and Conway, F.D.L. 2002. An investment in trust: communication in the commercial fishing and fisheries management communities. ORESU-G-01-004. Oregon Sea Grant, Oregon State University, Corvallis, Oreg.

Gillis, D.M., Peterman, R.M., and Pikitch, E.K. 1995. Implications of trip regulations for high-grading: a model of the behavior of fishermen. Can. J. Fish. Aquat. Sci. **52**: 402–415.

Goldfinger, C., Romsos, C., Robison, R., Milstein, R., and Myers, B. 2003. Interim seafloor lithology maps for Oregon and Washington. Version 1.0. [CD-ROM]. Active Tectonics and Seafloor Mapping Laboratory Publication 02-01. Oregon State University, Corvallis, Oreg.

Greene, H.G., Yoklavich, M.M., Starr, R.M., O'Connell, V.M., Wakefield, W.W., Sullivan, D.E., McRea, J.E., Jr., and Cailliet, G.M. 1999. A classification scheme for deep seafloor habitats. Oceanol. Acta, **22**: 663–678.

Hannah, R.W. 2003. Spatial changes in trawl fishing effort in response to footrope diameter restrictions in the US west coast bottom trawl fishery. N. Am. J. Fish. Manag. **23**: 693–702.

Hixon, M.A., Tissot, B.N., and Pearcy, W.G. 1991. Fish assemblages of rocky banks of the Pacific Northwest (Heceta, Coquille, and Daisy banks). Final Report OCS Study MMS 91-0052. USDI Minerals Management Service, Camarillo, Calif.

Holland, D.S. 2003. Integrating spatial management measures into traditional fishery management systems: the case of the Georges Bank multispecies groundfish fishery. ICES J. Mar. Sci. **60**: 915–929.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. **4**: 1–23.

Holling, C.S., Schindler, D.W., Walker, B., and Roughgarden, J. 1995. Biodiversity and the functioning of ecosystems: an ecological synthesis. *In* Biodiversity loss: ecological and economic issues. *Edited by* C. Perrings, K.G. Maler, C. Folke, C.S. Holling, and B.O. Jansson. Cambridge University Press, Cambridge, UK.

Jennings, S., and Kaiser, M.J. 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. **34**: 201–352.

Johnson, K.A. 2002. A review of national and international literature on the effects of fishing on benthic habitats. NOAA Tech. Memo. NMFS-F/SPO-57.

Kaiser, M.J., Collie, J.S., Hall, S.J., Jennings, S., and Poiner, I.R. 2002. Modification of marine habitats by trawling activities: prognosis and solutions. Fish Fish. **3**: 114–136.

Kaiser, M.J., Collie, J.S., Hall, S.J., Jennings, S., and Poiner, I.R. 2003. Impacts of fishing gear on marine benthic habitats. *In* Responsible fisheries in the marine ecosystem. *Edited by* M. Sinclair and G. Valdirmarsson. FAO, Cambridge, Mass.

Kaplan, I.M. 1998. Regulation and compliance in the New England conch fishery: case for co-management. Mar. Policy, **22**(4–5): 327–335.

Kemp, Z., and Meaden, G. 2002. Visualization for fisheries management from a spatiotemporal perspective. ICES J. Mar. Sci. **59**: 190–202.

Krost, P., Bernhard, M., Werner, F., and Hukriede, W. 1990. Otter trawl tracks in Kiel Bay (western Baltic) mapped by side-scan sonar. Meeresforschung, **32**: 344–353.

Kulka, D.W., and Pitcher, D.A. 2001. Spatial and temporal patterns in trawling activity in the Canadian Atlantic and Pacific. ICES CM 2001/R:02.

Larcombe, J.W.P., McLoughlin, K.J., and Tilzey, R.D.J. 2001. Trawl operations in the South East Fishery, Australia: spatial distribution and intensity. Mar. Freshw. Res. **52**: 419–430.

Love, M.S., Yoklavich, M., and Thorsteinson, L. 2002. The rockfishes of the northeast Pacific. University of California Press, Los Angeles, Calif.

Marrs, S.J., Tuck, I.D., Atkinson, R.J.A., Stevenson, T.D.I., and Hall, C. 2002. Position data loggers and logbooks as tools in fisheries research: results of a pilot study and some recommendations. Fish. Res. **58**: 109–117.

Matthews, K.R. 1989. A comparative study of habitat use by young-of-the-year, sub-adult, and adult rockfishes on four habitat types in Central Puget Sound. Fish. Bull. **88**: 223–239.

McCain, B. 2003. Revised appendix: essential fish habitat, west coast groundfish. National Marine Fisheries Service, Seattle, Wash.

McRea, J.E., Jr., Greene, H.G., O'Connell, V.M., and Wakefield, W.W. 1999. Mapping marine habitats with high-resolution sidescan sonar. Oceanol. Acta, **22**: 679–686.

Meaden, G.J. 2000. Applications of GIS to fisheries management. *In* Marine and coastal geographical information systems. *Edited by* D.J.Wright and D.J. Bartlett. Taylor and Francis Inc., Philadelphia, Pa. pp. 205–226.

Nasby-Lucas, N.M., Embley, R.W., Hixon, M.A., Merle, S.G., Tissot, B.N., and Wright, D.J. 2002. Integration of submersible transect data and high-resolution multibeam sonar imagery for a habitat-based groundfish assessment of Heceta Bank, Oregon. Fish. Bull. **100**: 739–751.

National Marine Fisheries Service. 2005. Pacific coast groundfish fishery management plan: essential fish habitat designation and minimization of adverse impacts. National Marine Fisheries Service, Northwest Region, Seattle, Wash.

National Research Council. 2000. Improving the collection, management, and use of marine fisheries data. National Academy Press, Washington, D.C.

© 2005 NRC Canada

National Research Council. 2002. Effects of trawling and dredging on seafloor habitat. National Academy Press, Washington, D.C.

National Research Council. 2004. Cooperative research in the National Marine Fisheries Service. National Academy Press, Washington, D.C.

Piet, G.J., Rijnsdorp, A.D., Bergman, M.J.N., van Stanbrink, J.W., Craeymeersch, J., and Buijs, J. 2000. A quantitative evaluation of the impact of beam trawling on benthic fauna in the southern North Sea. ICES J. Mar. Sci. **57**: 1332–1339.

Pikitch, E.K. 1987. Use of a mixed-species yield-per-recruit model to explore the consequences of various management policies for the Oregon flatfish fishery. Can. J. Fish. Aquat. Sci. **44**(Suppl. 2): 349–359.

Pitcher, C.R., Poiner, I.R., Hill, B.J., and Burridge, C.Y. 2000. Implications of the effects of trawling on sessile megazoobenthos on a tropical shelf in northeastern Australia. ICES J. Mar. Sci. **57**: 1359–1368.

Ragnarsson, S.A., and Steingrimsson, S.A. 2003. Spatial distribution of otter trawl effort in Icelandic waters: comparison of measures of effort and implications for benthic community effects of trawling activities. ICES J. Mar. Sci. **60**: 1200–1215.

Rijnsdorp, A.D., Buys, A.M., Storbeck, F., and Visser, E.G. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES J. Mar. Sci. **55**: 403–419.

Rijnsdorp, A.D., Piet, G.J., and Poos, J.J. 2001. Effort allocation of the Dutch beam trawl fleet in response to a temporarily closed area in the North Sea. ICES CM 2001/N:01.

Romsos, C. 2004. Mapping surficial geologic habitats of the Oregon continental margin using integrated interpretive and GIS techniques. M.S. thesis, Oregon State University, Corvallis, Oreg.

Sampson, D.B. 2001. An empirical analysis of fishing strategies derived from trawl logbooks. *In* Spatial processes and management of marine populations. *Edited by* G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Witherell. University of Alaska Sea Grant Program, Fairbanks, Alaska. Rep. No. AK-SG-01-02. pp. 539–541.

Sampson, D.B., and Crone, P.R. 1997. Commercial fisheries data collection procedures for US Pacific coast groundfish. NOAA Tech. Memo. NMFS-NWFSC-31.

Scholz, A., Mertens, M., Sohm, D., Steinback, C., and Bellman, M. 2005. Place matters: spatial tools for assessing the socioeconomic implications of marine resource management measures on the Pacific Coast of the United States. *In* Benthic habitats and the effects of fishing. Symposium 41. *Edited by* P.W. Barnes and J. Thomas. American Fisheries Society, Bethesda, Md. pp. 727–744.

Starr, R.M., and Fox, D.S. 1996. Comparison of commercial fishery and research catch data. Can. J. Fish. Aquat. Sci. **53**: 2681–2694.

Stein, D.L., Tissot, B.N., Hixon, M.A., and Barss, W. 1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. Fish. Bull. **90**: 540–551.

Valdemarsen, J.W., and Suuronen, P. 2003. Modifying fishing gear to achieve ecosystem objectives. *In* Responsible fisheries in the marine ecosystem. FAO, Cambridge, Mass.

Van Marlen, B. 2000. Technical modifications to reduce the bycatches and impacts of bottom fishing gears. *In* The effects of fishing on non-target species and habitats. *Edited by* M.J. Kaiser and S.J. de Groot. Blackwell Scientific Publications, Oxford, UK. pp. 198–216.

Yoklavich, M.M., Greene, H.G., Cailliet, G.M., Sullivan, D.E., Lea, R.N., and Love, M.S. 2000. Habitat associations of deep-water rockfishes in a submarine canyon: an example of a natural refuge. Fish. Bull. **98**: 625–641.

© 2005 NRC Canada

Canadian Journal of Fisheries and Aquatic Sciences

Author Index
Volume 62, 2005

Journal canadien des sciences halieutiques et aquatiques

Index des auteurs
Volume 62, 2005

Aanes, S., 1377
Aas-Hansen, Ø., 195
Abrams, P.A., 725, 738, 758
Adams, S., 679
Agostinho, A.A., 714
Aguilar, A., 1589
Ahlgren, G., 2240
Ainsworth, C.H., 1104
Alcala, A.C., 98
Alcaraz, C., 453
Aldrin, M., 1377
Alkanani, T., 2509
Allen, E.W., 1963
Àlvarez, D., 643, 2169
Ambrose, W.G., Jr., 1756
Andersen, T., 322
Anderson, C., 333
Anderson, D.S., 1905
Anderson, J.J., 1665, 2423
Argyle, R.L., 1432
Arjas, E., 291
Armstrong, D.A., 250, 2673
Armstrong, L.M., 991
Armsworthy, S., 1271
Arnott, S.A., 730
Arnott, S.E., 2450
Ashford, J.R., 2832
Astatkie, T., 2067
Atkinson, R.J.A., 2076
Baba, K., 2475
Bachmann, R.W., 2760
Baglinière, J.-L., 1600
Bailey, S.A., 1090, 2386, 2463
Baker, J.D., 1386
Baldigo, B.P., 1168
Ballantyne, F., 863
Ballantyne, J.S., 2661, 2854, 2864
Ballara, S.L., 593
Banks, J.D., 1589
Banks, M.A., 1874, 2189
Barbeau, M.A., 1766
Barnett-Johnson, R., 2425
Bartlett, A.J., 1243
Batchelor, S.P., 1243
Batterman, S.L., 1254
Baumgartner, M.F., 527
Begg, G.A., 679
Bellman, M.A., 2886
Bence, J.R., 436, 1432
Bennett, T.R., 2811
Bentley, N., 1553
Bentzen, P., 2519
Berglund, O., 1201, 2021
Bertolo, A., 2706
Bertram, D.F., 2841
Biagi, C.A., 1386
Bird, D.F., 2100
Bjornn, T.C., 30
Black, B.A., 2277
Blais, J.M., 236
Blanchard, J.L., 2001
Blanchfield, P.J., 2694
Blum, J.D., 48
Boberg, M., 2240
Bodaly, R.A., 991
Boehlert, G.W., 2277
Boeing, W.J., 1286
Bogazzi, E., 631
Boggs, C.H., 1320
Boggs, C.T., 930
Bograd, S.J., 1782
Boisclair, D., 1079
Bondar, C.A., 2632
Bondy, J., 2864
Bootsma, H., 1651
Borgmann, U., 1243
Botsford, L.W., 905, 1626
Bottriell, K., 2632
Bowlby, J.N., 700
Bowman, M.F., 174
Boyce, M.S., 2431
Bozek, M.A., 2110
Bradford, M.J., 2716
Branch, T.A., 631, 925
Brattey, J., 811
Brazner, J.C., 1254
Breien, M.T., 1822
Brettum, P., 322
Brodeur, P., 2211
Brodziak, J., 544
Bromaghin, J.F., 1570
Bronte, C.R., 482
Brooks, C., 2740
Budy, P., 2784
Bujold, V., 2443
Bundy, A., 1453, 1474
Bundy, M.H., 2371
Bunnell, D.B., 15, 2560
Burdett-Coutts, V., 1271
Burke, B.J., 930
Burns, D.A., 1168
Cabana, G., 333
Cahill, K.L., 2134
Cai, Y.R., 1019
Calumpong, H.P., 98
Cameron, C., 195
Campbell, L.M., 1161
Campbell, P.G.C., 563, 982
Canfield, D.E., Jr., 2760
Canino, M.F., 2519
Carr, G.M., 1309
Carreau, M., 1271
Caudill, C.C., 30
Chamberlain, C.P., 48
Chambers, P.A., 174, 1309
Charles, K., 1600
Chouinard, G.A., 1991
Claramunt, R.M., 2254
Clough, L.M., 1756
Coenders, G., 453
Colautti, R.I., 950
Collins, N.C., 738, 767, 2770
Conover, D.O., 730, 802
Conser, R.J., 1640
Cook, J.E., 2110
Cooke, S.J., 2124
Cossu-Leguille, C., 563
Courtemanche, D.A., 2443
Courtenay, S.C., 2055
Couture, P., 767
Cowan, J.H., Jr., 1337
Cox, M.K., 269
Craig, J.K., 1295
Crane, P.A., 1570
Cranford, P., 1271

© 2005 NRC Canada

Cristescu, M.E.A., 505
Crowder, L.B., 1295
Cucherousset, J., 1600
Culver, D.A., 205
Curry, R.A., 2443
Daigle, W.R., 930
Danila, D.J., 1611
Das, B., 1067
Dauble, D.D., 1513
Davies, C.R., 679
Davis, J.L.D., 109
Davis, L., 1410
DeAngelis, D.L., 781
Deng, R., 611
Deng, Z., 1513
Detenbeck, N.E., 1254
Dettman, D.L., 2874
Dettmers, J.M., 2010, 2683
de Valpine, P., 1937
DeVault, D.S., 482
Devlin, R.H., 1386
Dichmont, C., 611
Die, D., 611
Dieckmann, U., 811
Dillon, P.J., 1019
Dixon, D.G., 1243
Dobiesz, N.E., 1432
Dodson, J.J., 578
Donali, E., 322
Dorn, M.W., 925
Douglas, M.S.V., 2586
Drake, J.M., 1053
Driedzic, W.R., 2854, 2864
Drouillard, K.G., 464
Dufour, E., 2362
Duggan, I.C., 1090, 2463
Duhamel, G., 2832
Dunlop, E.S., 844, 1720
Duponchelle, F., 1651
Duston, J., 2067
Eastwood, P.D., 2001
Ebener, M.P., 482, 1432
Eckley, C.S., 400
Eckmann, R., 2294
Edwards, W.J., 205
Einhouse, D.W., 145
Einum, S., 1153
Elliott, B.J., 2254
Elsdon, T.S., 1143
Emmert, G.E., 2586
Enders, E.C., 1079
Engel, B.A., 1
English, K.K., 2124
Epperly, S.P., 965
Ernst, B., 250, 1665, 2423, 2673
Eshenroder, R.L., 1432
Essington, T.E., 1320, 1422
Evans, R.D., 1019
Everson, I., 2832
Fanning, L.P., 1474
Farrell, A.P., 2124
Faust, C.L., 2312
Feo, C., 453
Ficke, A.D., 2399
Field, J.C., 2199
Filippi, D., 1410
Findlay, D.L., 991
Fischer, P., 2294
Fisk, A.T., 1161
Fitzsimons, J.D., 2254
Fleming, I.A., 1153
Flessa, K.W., 2874
Floeter, J., 1853
Folkvord, A., 1037
Folt, C.L., 48
Foreman, M.G.G., 1350
Foster, D.G., 965
Fox, C.J., 2001
Freeman, M.C., 2312
Fresh, K.L., 2494
Frimpong, E.A., 1
Froglia, C., 2076
Fryer, B.J., 2609
Fuiman, L.A., 1337
Fukuda, A., 1410
Fukuwaka, M., 2752
Fulford, R.S., 2683
Futter, M.N., 2134
Gabos, S., 1963
Gagnon, J.E., 2609
Galarowicz, T.L., 2010, 2330
Gamperl, A.K., 2509
Garcia, P.S., 2811
García-Berthou, E., 453
Garton, D.W., 1119
Genna, R.L., 2675
Gerber, L.R., 863
Ghalambor, C.K., 791
Giani, A., 2100
Giguère, A., 563
Gillanders, B.M., 623, 1143
Glebe, B.D., 2661
Glémet, H., 2211
Goldfinger, C., 2886
Gomes, L.C., 714
Gomez-Uchida, D., 1874, 2189
Goodman, D., 374
Graeb, B.D.S., 2010
Graneli, W., 1201
Grant, J., 1271
Gravel, A., 982
Greenwood, J.L., 2033
Gresswell, R.E., 1797
Griffiths, D., 2796
Grift, R.E., 833
Grimes, C.B., 2425
Grønkjær, P., 2219
Gross, R., 1887
Gudmundsson, G., 1746
Guensch, G.R., 1513
Guenther-Gloss, P.M., 2399
Gunn, J.M., 2134
Haffner, G.D., 464
Hall, N., 611
Hamel, O.S., 1060
Hamer, P.A., 623
Hammill, M.O., 1991
Handegard, N.O., 2409
Hansen, L.P., 2502
Hard, J.J., 2538
Hare, L., 563
Harfenist, A., 2841
Hargrave, B., 1271
Haro, A., 68
Harrod, C., 2796
Hartman, K.J., 269
Harvey, B.C., 58, 650
Hauser, L., 2519
Havens, K.E., 348
Hawkins, L.A., 854
Haywood, M., 611
Healey, M.C., 2124
Hebert, P.D.N., 505
Heino, M., 811
Hendzel, L.L., 991
Heneberry, J., 341
Hennigar, A.W., 1766
Henwood, T.A., 1295
Heppell, S.A., 2886
Heppell, S.S., 863
Herricks, E.E., 1540
Higgins, P.S., 2716
Higuchi, H., 1410
Hilborn, R., 631, 1665, 1937, 1985, 2423
Hill, S.L., 2530
Hily, C., 123
Hinch, S.G., 2124
Hindar, A., 2620
Hines, A.H., 109
Hintelmann, H., 400
Hirst, D., 1377
Hofmann, E., 2832
Hogsden, K.L., 2226
Holland, D.S., 1553

© 2005 NRC Canada

Holmqvist, N., 1201
Hontela, A., 982
Höök, T.O., 2362
Horne, J.K., 2822
Horsburgh, C.A., 2760
Hoyer, M.V., 2760
Hrabik, T.R., 2177
Hrodey, P.J., 1
Huebert, D.B., 991
Huestis, S.Y., 464
Hugueny, B., 163
Huntington, C.W., 1920
Huryn, A.D., 1905
Huseby, R.B., 1377
Huser, B.J., 1702
Hutchings, J.A., 824, 1153
Hutchinson, C.E., 1060
Hvingel, C., 1833
Hyun, S.-Y., 1665, 2423
Ianelli, J.N., 1865
Ibarra, D., 1271
Interlandi, S.J., 1681
Jackson, L.J., 2088
Jacobson, L.D., 1640, 1782
Jager, H.I., 1733
Jagger, L.A., 1254
Jansen, W.A., 991
Janssen, J., 2683
Jenkins, G.P., 623
Jenkins, P.T., 1090, 2463
Jennings, M.J., 2110
Jennings, S., 2001
Jensen, D.A., 482
Jepson, M.A., 930
Johnsen, H.K., 195
Johnson, B.R., 301
Johnson, J.E., 1432
Johnson, L.E., 578
Johnson, S.L., 412
Johnson, S.P., 2285
Johnson, T.B., 15
Jonas, J.L., 2254
Jones, C.M., 2832
Jones, L.A., 1953
Jones, M.L., 1580
Jones, S.R.M., 2124
Jonsson, B., 2502
Jonsson, N., 2502
Jorgensen, J.C., 2343, 2354
Jørgensen, E.H., 195
Jørgensen, O.A., 1833
Jowett, I.G., 7
Jude, D.J., 2683
Jurado-Molina, J., 1865
Kaartvedt, S., 1822
Kaiser, M.J., 1194
Kalinowski, S.T., 693
Kamunde, C.N., 390
Kaplan, D.M., 905
Kaplan, I.C., 1710
Kasai, A., 671
Kasian, S.E.M., 991
Kaste, Ø., 312, 322
Kavanagh, K., 518
Keefer, M.L., 30, 930
Keeley, E.R., 1523
Keller, W., 341
Kelly, N.M., 2740
Kempf, A., 1853
Kennedy, B.P., 48
Kent, A.D., 400
Kitchell, J.F., 1320, 2159, 2343, 2354
Klug, J.L., 472
Knight, C.T., 15
Knox, D., 1363
Köck, G., 1161
Koen-Alonso, M., 1490
Kolesar, S.E., 1386
Koljonen, M.-L., 1887, 2143
Korman, J., 2716
Koskiniemi, J., 1887
Kottas, A., 1808
Kovalcik, P.A., 2371
Kövecses, J., 153
Koyama, A., 518
Kraak, S.B.M., 833
Krueger, D.M., 2177
Kuchel, L.J., 2124
Lacroix, G.L., 1363
LaHood, E., 1386
Lallemand, P., 1553
Lamouroux, N., 7
Langerhans, R.B., 2802
LaRose, J., 738
Larsson, P., 1201, 2021
Larsson, S., 2124
Lavrentyev, P.J., 2371
Lawrence, J.F., 2100
Lawson, P.W., 1920
Layman, C.A., 2802
Leduc, J., 341
Lee, J.G., 1
Lee, S.R., 930
Lee, Y.-W., 362
Legault, C.M., 544
Leiter, T., 1691
Lek, S., 2294
Le Loc'h, F., 123
Le Master, D.C., 1
Leonard, N.J., 2649
Lessard, B., 1320
Lester, N.P., 738
Levesque, H.M., 2854, 2864
Levin, P.S., 961
Levine, K.F., 1589
Lewis, M.A., 2386
Li, J.L., 1797
Lika, K., 425
Lilly, G.R., 811
Lim, K.J., 1
Limén, H., 2463
Lindner, G., 1691
Litt, A.H., 2494
Livingston, P.A., 1865
Lobón-Cerviá, J., 1231, 2484
Loftus, W.F., 781
Lohse, K.A., 2740
Lotto, A., 2124
Lou, D.C., 679
Løvik, J.E., 322
Lowe, R.L., 1905
Lozano, S.J., 482
Ludsin, S.A., 2609
Lyche-Solheim, A., 312, 322
Macdonald, J.S., 2124
MacFarlane, R.B., 2425
MacIsaac, H.J., 1090, 2386, 2463
MacIsaac, P.F., 2067
Mackie, P., 2661
MacLellan, S.E., 2265
Mafuka, J., 1651
Magnan, P., 747, 2706
Maguire, R.J., 1243
Makarewicz, J.C., 1432
Malinen, T., 245
Mandere, D., 1651
Mangel, M., 1219, 1808
Mäntyniemi, S., 291
Mapstone, B.D., 679
Marchand, F., 1600
Marschall, E.A., 2649
Marsden, J.E., 2254
Marshall, A.R., 1386
Martell, S.J.D., 215, 1320
Masuda, M., 2143
Mate, B.R., 527
Matsuda, H., 758, 2752
Maxwell, M.R., 1640
Mayo, M.R., 1386
Maypa, A.P., 98
McClelland, E.K., 2538
McCormick, S.D., 68
McDonald, E., 205
McHugh, P., 2784
McKinstry, C.A., 1513

© 2005 NRC Canada

McLeish, D.A., 1432
McMahon, T.E., 79
Meager, J.J., 1978
Meili, M., 2727
Melancon, S., 2609
Meldrup, D., 2219
Mello, L.G.S., 659
Mendelssohn, F., 1782
Menkel, J.L., 1060
Mereniender, A.M., 2740
Metcalfe, N.B., 2169
Méthot, G., 348
Meyer, J.L., 2312
Michel, T.J., 1681
Millar, R.B., 1028
Miller, J.A., 2189
Miller, T.J., 2560
Mills, C., 2001
Mills, E.L., 145
Mills, R.B., 1019
Milne, S.W., 1210
Milton, D., 611
Mingelbier, M., 2211
Minte-Vera, C.V., 925
Mitsutani, N., 2475
Modin, J., 1184
Mohr, L.C., 1432
Møller, P.R., 1833
Montoya, J.P., 1119
Moon, T.W., 2854, 2864
Moore, J.W., 2285
Moore, P.G., 2076
Morales-Baquero, R., 2640
Mordue (Luntz), A.J., 2675
Mordue, W., 2675
Morehead, N.R., 2586
Morello, E.B., 2076
Moreno, C., 2832
Morgan, G., 738
Morgan, M.J., 811
Morin, A., 1309
Morita, K., 2752
Morita, S.H., 2752
Morley, S.A., 2811
Morrison, J., 1350
Morrison, K., 400
Msukwa, A., 1651
Mudroch, A., 2586
Mueller, R.P., 1513
Muir, D.C.G., 1161
Munch, S.B., 730, 802, 1808
Munro, A.R., 79
Murdoch, P.S., 1168
Myers, J.M., 2538
Myers, R.A., 1130
Naish, K.A., 2538
Nakamoto, R.J., 58, 650
Nakayama, K., 671
Nalepa, T.F., 1432
Naughton, G.P., 30
Newbrey, M.G., 2110
Nichols, J.W., 2303
Nicieza, A.G., 643
Nickelson, T.E., 412, 1920
Nielsen, E.E., 2219
Nilsson, J., 1887
Nislow, K.H., 48
Niyogi, S., 390
North, A.W., 2530
Nyström, P., 1201, 2021
Oberdorff, T., 163
O'Brien, C.M., 2001
Oen, T., 1978
O'Farrell, M.R., 1626
Okada, E.K., 714
Oldman, J., 593
Olsen, E.M., 811
Ombredane, D., 1600
O'Neal, J.P., 1337
Onsrud, M.S.R., 1822
Oosterhout, G.R., 1920
Opperman J.J., 2740
O'Reilly, P.T., 2519
Orendorff, J.A., 1720
Orensanz, J.M., 250, 2673
Palen, W.J., 2285
Palmer, M.E., 1111
Papandroulakis, N., 425
Park, L.K., 1386, 2538
Parker, S.M., 1905
Parker Stetter, S.L., 145
Parkinson, E.A., 1523
Parrish, C.C., 2509
Parrish, R.H., 1782
Paterson, G., 464
Patterson, D.A., 2124
Patterson, W.P., 700, 2362
Paulsen, H., 2219
Payne, C.D., 1119
Pedersén, M., 2240
Peery, C.A., 30, 930
Pella, J.J., 2143
Peltonen, H., 245
Persaud, A.D., 483
Peterson, B.J., 1905
Petzold, M.M., 482
Pientka, B., 2683
Pihl, L., 1184
Pike, A.W., 2675
Pinel-Alloul, B., 348
Piner, K.R., 1060
Pinto-Coelho, R., 348
Plante, M., 747
Playle, R.C., 2303
Poirier, G.A., 1991
Polivka, K.M., 913
Pont, D., 163
Pou-Rovira, Q., 453
Prairie, Y.T., 2100
Prepas, E.E., 1963
Proulx, R., 747
Pulido-Villena, E., 2640
Purchase, C.F., 738, 2770
Quinn, T.J., II, 436
Rackham, B.D., 2001
Radomski, P., 436
Rajotte, J.W., 767
Ralston, S., 2199
Ramcharan, C.W., 1286
Ramos, F.C., 2425
Rasmussen, J.B., 153
Reavie, E.D., 2586
Reche, I., 2640
Regnell, O., 400
Rehmann, C.R., 205
Reid, K., 2530
Reinisch, C.L., 2055
Renaud, P.E., 1756
Rennie, M.D., 767, 2088, 2770
Reyjol, Y., 2294
Reynolds, J.D., 854
Reznick, D.N., 791
Ribbink, A.J., 1651
Ricciardi, A., 1111, 1953
Richards, C., 482
Richards, L.A., 593
Richardson, J.S., 2632
Richmond, M.C., 1513
Ridgway, M.S., 844, 1720, 2694
Rier, S.T., 185
Rijnsdorp, A.D., 833
Riley, S.C., 1400
Ripley, T., 2431
Rivard, B., 1067
Robbins, J.A., 2586
Robinson, A., 518
Robinson, C.L.K., 1350
Robinson, S.M.C., 1766
Robison, B.D., 2046
Rochet, M.-J., 224
Rodd, F.H., 1720
Rodgers, J.D., 412
Rodnick, K.J., 2509
Romakkaniemi, A., 291
Román, M., 2874

© 2005 NRC Canada

Romero, N., 1797
Roni, P., 2811
Rösch, R., 2294
Rose, G.A., 659
Rose, K.A., 886
Rosemond, A.D., 2033
Rosenfeld, J.S., 1691
Rothman, L., 1691
Rowell, K., 2874
Rowland, W., 2046
Roy, A.G., 1079
Roy, A.H., 2312
Rudstam, L.G., 145
Russ, G.R., 98
Rutherford, E.S., 2362
Ruzycki, J.R., 79
Rydin, E., 1702
Säisä, M., 1887
Sakhrani, D.M., 1386
Sala, E., 863
Sampson, D.B., 362
Sanchez-Azofeifa, A., 1067
Sanderson, B.L., 961
Saros, J.E., 1681
Sasaki, M., 2475
Sass, G.G., 2159
Scheuerell, J.M., 2494
Scheuerell, M.D., 961, 2494
Scheurer, J.A., 1400
Schindler, D.E., 2285, 2494
Schindler, D.W., 174
Schofield, B., 1271
Schreiner, D.R., 482
Schrum, C., 1853
Schwartz, J.S., 1540
Schwing, F.B., 1782
Scrimgeour, G., 2431
Setiawan, A., 1410
Shah, A.K., 965
Shanks, A.L., 2189
Shepherd, J.H., 2494
Sherwood, G.D., 153
Short, C., 2854, 2864
Shrimpton, M., 2124
Shuter, B.J., 725, 738, 767, 844, 1210, 1720
Sibley, T.H., 2494
Simon, T.P., 1
Simpson, M.J., 2010
Sirois, P., 578
Slavik, K.A., 1905
Sliva, L., 276
Smith, B.D., 2841
Smith, K.L., 1580
Smith, M.E., 1337
Snarski, V.M., 1254
Snoeijs, P., 2240
Snover, M.L., 1219
Solazzi, M.F., 412
Solbakken, T., 1978
Sprules, W.G., 1210
Stamford, M.D., 2548
Stark, S.L., 1254
Stein, R.A., 2649
Steinhart, G.B., 2649
Stenroth, P., 1201
Stephens, R.E., 2055
Stewart, D.J., 700
Stewart, I.J., 925
Stewart, T.J., 700
Stewart, W.S., 1028
St-Jean, S.D., 2055
Stoermer, E.F., 2586
Storvik, G., 1377
Strachan, W.M.J., 1963
Stransky, C., 2265
Strecker, A.L., 2450
Stuehrenberg, L.C., 30
Sumaila, U.R., 1104
Sundbom, M., 2727
Sutton, T.M., 1
Suzuki, K.W., 671
Suzuki, M., 1410
Swain, D.P., 1991
Tähtinen, J., 1887
Tanaka, M., 671
Tanner, D.K., 1254
Taper, M.L., 693
Tardif, D., 2211
Tatara, C.P., 1400
Taylor, D.L., 1611
Taylor, E.B., 1523, 2548
Taylor, N.G., 215
Temming, A., 1853
Tjøstheim, D., 2409
Tolotti, K.R., 930
Treble, M.A., 1833
Tremblay, A., 2770
Trenkel, V.M., 224
Trevorrow, M.V., 1004
Trexler, J.C., 781
Tuchman, N.C., 185
Tuomaala, A., 245
Turner, M.A., 991
Uh, M., 1386
Utne-Palm, A.C., 1978
Vadeboncoeur, Y., 1422
Vance, D., 611
Van Der Kraak, G., 2124
Vanderploeg, H.A., 2371
Vander Zanden, M.J., 1422
Van Nieuwenhuyse, E.E., 492
Van Nieuwerburgh, L., 2240
van Overdijk, C.D.A., 2463
Vascotto, K., 738
Vasemägi, A., 1887
Vijayan, M.M., 195
Vinebrooke, R.D., 1067, 2226
Vinther, M., 1853
Wagner, G.N., 2124
Wahl, D.H., 2010, 2330
Wallace, J.B., 301
Wallace, J.R., 1060
Walline, P.D., 2822
Walsh, M.R., 730, 802
Walters, C.J., 215, 1320, 1985
Wang, X., 1161
Wänstrand, I., 2240
Ward, P., 1130
Watras, C.J., 400
Watson, J.W., 965
Watters, G.M., 1219
Waugh, S., 1410
Wayne, R.K., 1589
Webb, T.J., 854
Weir, L.K., 1153
Welch, D.W., 133
Wennhage, H., 1184
Wetzel, R.G., 185
White, J.L., 58, 650
Whitehead, H., 2573
Whittle, D.M., 464
Whoriskey, F.G., Jr., 2443
Williams, A.J., 679
Williams, D.D., 276
Williams, J.G., 961
Williams, R., 2832
Wilzbach, M.A., 58
Wimmer, T., 2573
Winder, M., 2285
Winemiller, K.O., 872, 2802
Winkler, G., 578
Winter, A.R., 2303
Wissel, B., 1286
Witzel, L.D., 145
Woldt, A.P., 1432
Wolfe, A.P., 1067, 1681
Wong, M.C., 1766
Wonham, M.J., 2386
Wood, C.M., 390
Wright, P.A., 2661
Wright, R.F., 2620
Wu, F.C., 1019
Wurster, C.M., 700
Yan, N.D., 483

© 2005 NRC Canada

Yang, Z., 2609
Yodzis, P., 1490
Yoklavich, M.M., 2277
Young, M.K., 2399
Young-Williams, A.C., 109
Zabel, R.W., 961
Zamon, J.E., 133
Zamora, L., 453
Zeldis, J.R., 593
Zeron, K., 2632
Zhang, W., 1963
Zimmerman, C.E., 88
Zohar, Y., 109
Zydlewski, G.B., 68

© 2005 NRC Canada

The index and/or table of contents has been removed and photographed separately within this volume year.

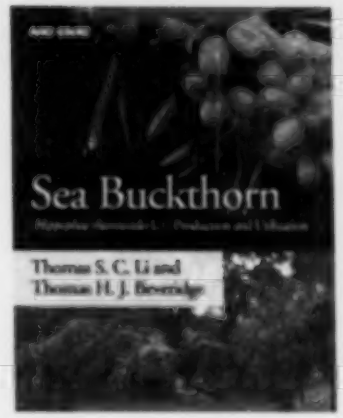
For roll film users, this information for the current volume year is at the beginning of the microfilm. For a prior year volume, this information is at the end of the microfilm.

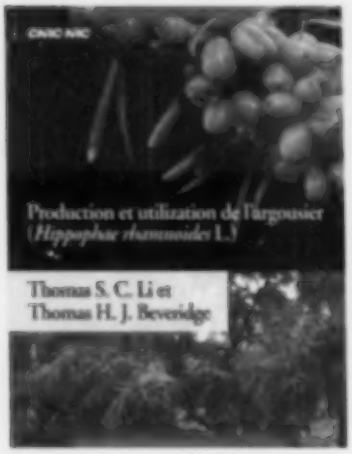
For microfiche users, the index and/or contents is contained on a separate fiche.

Sea Buckthorn (*Hippophae rhamnoides L.*): Production and Utilization

By T.S.C. Li and T.H.J. Beveridge

137 Pages 2003
Softcover
ISBN 0-660-19007-9
NRC 46317
$44.95 CAN. Other countries $44.95 US
Canadian customers add GST (7%)





Production et utilisation de l'argousier *(Hippophae rhamnoides L.)*

Par T.S.C. Li et T.H.J. Beveridge

140 Pages 2004
Édition brochée
ISBN 0-660-96931-9
CNRC 46841
44,95 $CAN. À l'étranger 44,95 $US
Clients du Canada, ajoutez la TPS (7 %)

Orders may be submitted by mail or fax to:
Les commandes peuvent être soumises par courrier ou par télécopieur à :

Order Office / Bureau des commandes

NRC Research Press / Presses scientifique du CNRC
National Research Council / Conseil national de recherches
Ottawa, ON K1A 0R6, Canada
Telephone / Téléphone : (613) 990-2254
Fax / Télécopieur : (613) 952-7656
E-mail / Courriel : pubs@nrc-cnrc.gc.ca
Website / Site web : http://pubs.nrc-cnrc.gc.ca

PLEASE PRINT/LETTRES MOULÉES

☐ Payment enclosed / Paiement inclus ☐ Charge to/ Imputer à ☐ Visa ☐ MasterCard

Account no./N° de compte Expiry date/Date d'expiration

Name/Nom

Signature

Address/Adresse

City/Ville Province

Postal code/Code postal Country/Pays

Telephone/Téléphone Fax/Télécopieur

E-mail/Courriel:

Prepayment required unless order is accompanied by a purchase order number. Cheques or money orders should be made payable to : "Receiver General for Canada, Credit NRC". All sales are final.
Les commandes doivent être payées d'avance à moins qu'elles ne soient accompagnées d'un numéro de bon de commande. Les chèques ou mandats doivent être libellés au « Receveur général du Canada, crédit du CNRC ». Toutes les ventes sont finales.

Fisheries and Aquatic Sciences
Sciences halieutiques et aquatiques

Photographic Atlas of Fish Otoliths of the Northwest Atlantic Ocean
By / Par Stephen E. Campana

$54.95 CAN. Other countries $54.95 US
54,95 $CAN. À l'étranger 54,95 $US
Softcover / Édition brochée
(*Can. Spec. Publ. Fish. Aquat. Sci. / Publ. spéc. can. sci. halieut. aquat. 133*)
284 pages ISBN 0-660-19108-3 ISSN 0706-6481 NRC / CNRC 46328

Salmonine Introductions to the Laurentian Great Lakes:
An Historical Review and Evaluation of Ecological Effects
By / Par Stephen S. Crawford

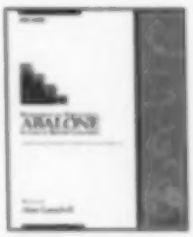
$42.95 CAN. Other countries $42.95 US
42,95 $CAN. À l'étranger 42,95 $US
Softcover / Édition brochée
(*Can. Spec. Publ. Fish. Aquat. Sci. / Publ. spéc. can. sci. halieut. aquat. 132*)
215 pages ISBN 0-660-17639-4 ISSN 0706-6481 NRC / CNRC 42734

Marine Protected Areas and Fisheries Closures in British Columbia
By Glen S. Jamieson and Joanne Lessard

$69.95 CAN. Other countries $69.95 US
69,95 $CAN. À l'étranger 69,95 $US
Softcover / Édition brochée
(*Can. Spec. Publ. Fish. Aquat. Sci. / Publ. spéc. can. sci. halieut. aquat. 131*)
414 pages ISBN 0-660-17788-9 ISSN 0706-6481 NRC / CNRC 42846

Workshop on Rebuilding Abalone Stocks in British Columbia
By / Par Alan Campbell

$42.95 CAN. Other countries $42.95 US
42,95 $CAN. À l'étranger 42,95 $US
Softcover / Édition brochée
(*Can. Spec. Publ. Fish. Aquat. Sci. / Publ. spéc. can. sci. halieut. aquat. 130*)
158 pages ISBN 0-660-18292-0 ISSN 0706-6481 NRC / CNRC 42841



To order any of the above titles / Commandez n'importe quel titre ci-dessus à :

Telephone / Téléphone : (613) 990-2254
Fax / Télécopieur : (613) 952-7656
E-mail / Courriel : pubs@nrc-cnrc.gc.ca
Web site / Site web : http://pubs.nrc-cnrc.gc.ca

Order Office / Bureau des commandes
NRC Research Press / Presses scientifique du CNRC
National Research Council / Conseil national de recherches
Ottawa, ON K1A 0R6, Canada

Canadian customers add GST (7%). Prepayment required unless order is accompanied by a purchase order number. Cheques or money orders should be made payable to : "Receiver General for Canada, Credit NRC". For all orders outside Canada, rates are in U.S. Dollars. All sales are final.
Clients du Canada, ajoutez la TPS (7 %). Les commandes doivent être payées d'avance à moins qu'elles ne soient accompagnées d'un numéro de bon de commande. Les chèques ou mandats doivent être libellés au « Receveur général du Canada, crédit du CNRC ». Pour les commandes hors-Canada, les tarifs sont en dollars américains. Toutes les ventes sont finales.

Chris Harrod and David Griffiths	**2796–2801**	Parasitism, space constraints, and gonad asymmetry in the pollan (*Coregonus autumnalis*)
C.A. Layman, R.B. Langerhans, and K.O. Winemiller	**2802–2810**	Body size, not other morphological traits, characterizes cascading effects in fish assemblage composition following commercial netting
Sarah A. Morley, Patricia S. Garcia, Todd R. Bennett, and Philip Roni	**2811–2821**	Juvenile salmonid (*Oncorhynchus* spp.) use of constructed and natural side channels in Pacific Northwest rivers
John K. Horne and Paul D. Walline	**2822–2831**	Spatial and temporal variance of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea
J.R. Ashford, C.M. Jones, E. Hofmann, I. Everson, C. Moreno, G. Duhamel, and R. Williams	**2832–2840**	Can otolith elemental signatures record the capture site of Patagonian toothfish (*Dissostichus eleginoides*), a fully marine fish in the Southern Ocean?
Douglas F. Bertram, Anne Harfenist, and Barry D. Smith	**2841–2853**	Ocean climate and El Niño impacts on survival of Cassin's Auklets from upwelling and downwelling domains of British Columbia
H.M. Levesque, C. Short, T.W. Moon, J.S. Ballantyne, and W.R. Driedzic	**2854–2863**	Effects of seasonal temperature and photoperiod on Atlantic cod (*Gadus morhua*). I. Morphometric parameters and metabolites
H.M. Levesque, J. Bondy, C. Short, J.S. Ballantyne, W.R. Driedzic, and T.W. Moon	**2864–2873**	Effects of seasonal temperature and photoperiod on Atlantic cod (*Gadus morhua*). II. Enzymes of intermediary metabolism
Kirsten Rowell, Karl W. Flessa, David L. Dettman, and Martha Román	**2874–2885**	The importance of Colorado River flow to nursery habitats of the Gulf corvina (*Cynoscion othonopterus*)
Marlene A. Bellman, Scott A. Heppell, and Chris Goldfinger	**2886–2900**	Evaluation of a US west coast groundfish habitat conservation regulation via analysis of spatial and temporal patterns of trawl fishing effort

Author Index for Volume 62	AI-1	Index des auteurs pour le volume 62	AI-1
Contents for Volume 62	C-1	Sommaire pour le volume 62	C-1

National Research Council Canada
Ottawa, Canada K1A 0R6

Conseil national de recherches Canada
Ottawa, Canada K1A 0R6

Postage paid at Ottawa
Publications mail
Registration No. 40062591

Port payé à Ottawa
Poste-publication
Enregistrement n° 40062591

USPS periodical postage paid at Champlain, NY 12919, USA

Canadian Journal of Fisheries and Aquatic Sciences

Volume 62, Number 12, December 2005

Journal canadien des sciences halieutiques et aquatiques

Volume 62, numéro 12, décembre 2005

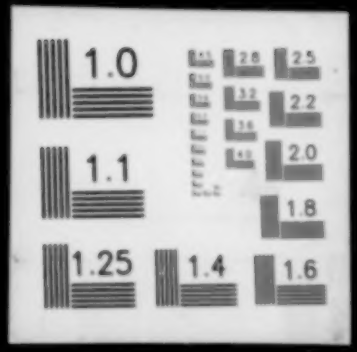
ARTICLES		ARTICLES
R.L. Genna, W. Mordue, A.W. Pike, and A.J. Mordue (Luntz)	2675–2682	Light intensity, salinity, and host velocity influence presettlement intensity and distribution on hosts by copepodids of sea lice, *Lepeophtheirus salmonis*
John M. Dettmers, John Janssen, Bernard Pientka, Richard S. Fulford, and David J. Jude	2683–2693	Evidence across multiple scales for offshore transport of yellow perch (*Perca flavescens*) larvae in Lake Michigan
Paul J. Blanchfield and Mark S. Ridgway	2694–2705	The relative influence of breeding competition and habitat quality on female reproductive success in lacustrine brook trout (*Salvelinus fontinalis*)
Andrea Bertolo and Pierre Magnan	2706–2715	The relationship between piscivory and growth of white sucker (*Catostomus commersoni*) and yellow perch (*Perca flavescens*) in headwater lakes of the Canadian Shield
Michael J. Bradford, Josh Korman, and Paul S. Higgins	2716–2726	Using confidence intervals to estimate the response of salmon populations (*Oncorhynchus* spp.) to experimental habitat alterations
Marcus Sundbom and Markus Meili	2727–2739	Ecophysiological determinants of the variation in ^{137}Cs concentrations between and within lacustrine fish populations
Jeff J. Opperman, Kathleen A. Lohse, Colin Brooks, N. Maggi Kelly, and Adina M. Merenlender	2740–2751	Influence of land use on fine sediment in salmonid spawning gravels within the Russian River Basin, California
Kentaro Morita, Shoko H. Morita, Masa-aki Fukuwaka, and Hiroyuki Matsuda	2752–2759	Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus* spp.
Mark V. Hoyer, Christine A. Horsburgh, Daniel E. Canfield, Jr., and Roger W. Bachmann	2760–2769	Lake level and trophic state variables among a population of shallow Florida lakes and within individual lakes
M.D. Rennie, N.C. Collins, C.F. Purchase, and A. Tremblay	2770–2783	Predictive models of benthic invertebrate methylmercury in Ontario and Quebec lakes
Peter McHugh and Phaedra Budy	2784–2795	An experimental evaluation of competitive and thermal effects on brown trout (*Salmo trutta*) and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) performance along an altitudinal gradient

Continued on inside back cover / Suite au verso

Canada

Printed in Canada by / Imprimé au Canada par
NRC Reprographic Services / Service de reprographie CNRC
Page production by / Mise en page par
NRC Research Press / Presses scientifiques du CNRC

0706-652X(200512)62:12;1-U


1.0
1.1
1.25
1.4
1.6
2.0
2.2
2.5